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Drift-Bottle Experiments in the Quoddy Region, Bay of Fundy[1,2]

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ABSTRACT

In conjunction with the research program of the International Passamaquoddy Fisheries Board, approximately 10,000 drift bottles were released in the Quoddy Region of the Bay of Fundy in 1957 and 1958. Overall return of bottles was 25%. Results have been analyzed and surface drift inferred on monthly and seasonal bases. On the average, there is a counter-clockwise circulation in Passamaquoddy Bay, an outflow through Western Passage, a variable flow in Letite Passage, an outflow on the Campobello side and an inflow along the Deer Island side of Head Harbour Passage. In the outer Quoddy Region, there is evidence of a clockwise circulation around The Wolves, a variable flow in Grand Manan Channel, and a southerly movement off the east coast of Grand Manan Island.

Wind speed and direction, which vary seasonally, appear very effective in altering the pattern of drift.

INTRODUCTION

Studies of the physical oceanography of the Quoddy Region and contiguous areas of the Bay of Fundy and the Gulf of Maine (Fig. 1) were undertaken in 1957 and 1958 as part of the International Passamaquoddy Fisheries Investigations (Hart and McKernan, 1960). Observations included temperatures, salinities, dissolved oxygen, tidal streams and non-tidal circulation. This report deals with the studies of non-tidal circulation.

Over a period of approximately 40 years, drift-bottle experiments were carried out intermittently in the Bay of Fundy and the Gulf of Maine areas in order to determine gross features of surface circulation. Mavor (1922) studied the results of drift-bottle experiments carried out in 1919. He made use of Dawson's (1908) current-meter data for the Bay of Fundy to assist in plotting pathlines of drift bottles. During the 1920's, extensive experiments were organized on a co-operative basis through the North American Council on Fisheries Investigations. While most of the releases were outside the Bay of Fundy region, those in the Yarmouth and Cape Sable areas (Bigelow, 1927; Atlantic Oceanographic Group, MS, 1958) provided useful information about the inflow of water to the Bay of Fundy. Hachey and Huntsman (MS, 1927) undertook drift-bottle experiments in Passamaquoddy Bay. Distribution of recovery localities for the somewhat over 50% of liberated bottles recovered led to the conclusion that there

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was a counter-clockwise circulation in the bay. Hachey and Bailey (MS, 1952) presented results of drift-bottle experiments carried out in 1930. From temperature and salinity observations combined with information provided by bottles released in five areas, mostly within the Quoddy Region, these workers concluded that circulation in the main part of the Bay of Fundy is in a counter-clockwise direction, while waters around Grand Manan circulate in a clockwise direction. Bailey (MS, 1957) constructed a diagram, derived from drift-bottle experiments and density distributions, showing the general circulation in the Quoddy Region. He suggested a counter-clockwise movement in Passamaquoddy Bay, an inward movement through Letite Passage, and an outward movement through Western Passage. In Grand Manan Channel, waters near the coast of Maine have an outward movement while those on the Grand Manan Island side have an inward movement. A clockwise circulation around The Wolves was inferred.

The afore-mentioned studies constitute the bulk of direct measurements of surface circulation that were undertaken in the Bay of Fundy region prior to 1957. In all cases, observations were limited to part of the year and frequently to only part of the Quoddy Region at any one time. Further information was needed concerning the overall pattern of drift and the variations, if any, from season to season. The purpose of the present drift-bottle project was to provide, in part, this needed information.

Throughout this paper, "winter" refers to the months of January, February and March; "spring" to April, May and June; "summer" to July, August and September; and "autumn" to October, November and December.

DESCRIPTION OF THE AREA

The 1957 and 1958 drift-bottle project was conducted in the Quoddy Region, which is defined as lying inshore of lines connecting West Quoddy Head, Maine, and Point Lepreau, N.B., to the northern tip of Grand Manan Island (Fig. 1). For convenience, the region is divided into five parts; Passamaquoddy Bay, passages, Cobscook Bay, outer Quoddy Region, and Grand Manan Channel.

Passamaquoddy Bay

Passamaquoddy Bay is almost enclosed by land. It receives fresh water from the St. Croix, the Magaguadavic, and Digdeguash Rivers (Fig. 1). Total mean discharge of fresh water is approximately 4,000 ft^3/sec (Forgeron, MS, 1959) of which more than one half is supplied by the St. Croix River. Passamaquoddy Bay and the St. Croix estuary have an average depth of 78 and 39 feet (ft), respectively. Throughout this report, depths are referred to mean low water. The coastline of Passamaquoddy Bay is approximately 120 nautical miles (naut mi) long including St. Croix estuary and Western Passage. The total area of the bay is 65 square nautical miles (sq naut mi). The bay is shallow in the northern part and becomes progressively deeper toward the passages. A

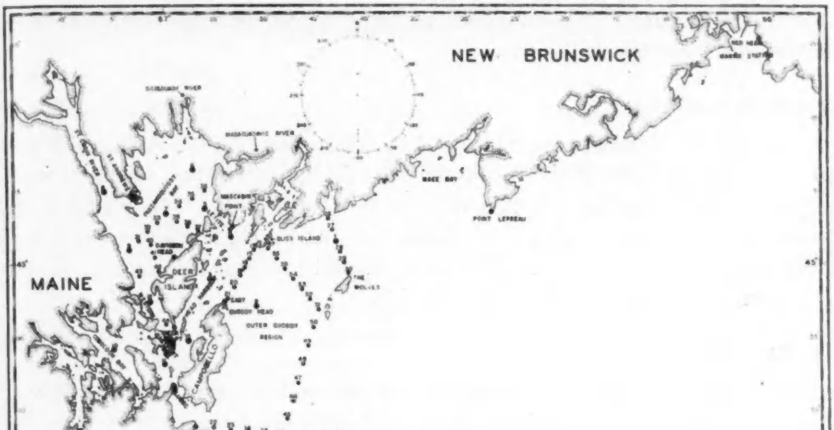


FIG. 1. Map of area showing location of Quoddy Project stations and wind observation stations.

basin exists inside the bay near Letite Passage with a maximum depth of 240 ft. A similar depression exists near Western Passage with a maximum depth of 240 ft within the bay and becoming progressively deeper in the passage.

PASSAGES

Passamaquoddy Bay is connected with the Bay of Fundy by Western, Letite, Little Letite, Doyle, and Head Harbour Passages. Cobscook Bay is connected with the Bay of Fundy by Friar Roads, Head Harbour Passage and Lubec Narrows. Western Passage and its extension, Head Harbour Passage, is relatively long and deep. Channel depths vary, approximately, from 180 to 390 ft. Letite Passage is short, tortuous and dotted with shoals and islands. Channel depths range from less than 100 to greater than 250 ft. Little Letite and Doyle Passages and Lubec Narrows are very shallow and allow passage of only a minor part of the intertidal volume.

COBSCOOK BAY

Cobscook Bay, an irregular-shaped body of water, with a coastline of approximately 135 naut mi, encloses 29 sq naut mi and has an average depth of

26 ft. The average freshwater discharge for 1956 and 1957 was computed to be 300 ft^3/sec (Forgeron, MS, 1959).

Outer Quoddy Region

This region includes waters bounded by the passages on the inshore side and by a line running from West Quoddy Head to Long Eddy Point, Grand Manan, thence to Point Lepreau, N.B., on the offshore side (Fig. 1). Many islands are located at the approaches to and in the passages, and cause much turbulence and a complex surface circulation. The outer Quoddy Region has an area of 210 sq naut mi. Depths range from 30 to 500 ft.

Grand Manan Channel

This passage separates Grand Manan Island from the State of Maine. The Grand Manan coast consists of high land and cliffs rising abruptly from the sea. There are no significant bays or harbours. The Maine coast is also abrupt, but contains many harbours and indentations. Width of the channel at the southern end is approximately 13 naut mi and at the northern end 6 naut mi. The channel itself has a fairly level floor, with depths mostly between 240 and 300 ft. A small channel runs into the northern end with depths as great as 360 ft. Across much of the southern end there are many shoals, rocks, ledges, and small islands. Grand Manan Channel and the region southwestward have strong tidal currents and the water is extremely well mixed.

METHOD FOR DETERMINING RESIDUAL FLOW

There are two methods for making direct measurements of currents: one method, using current meters, measures the flow of water past a given point in space; the second involves tracking drifting objects such as bottles, buoys and drogues.

To determine residual flow which is the flow remaining after removal of tidal-stream components, measurements of currents over a complete tidal cycle are required. This makes the operation of current meters, which must be held fixed either from an anchored ship or by anchoring separately, extremely laborious for determining residual flow over an extensive area. Moreover, unless a large number of measurements can be taken at one time, results are not synoptic, and questions as to validity in assuming them synoptic in coastal areas place limitations on their significance. Valuable information can frequently be obtained by releasing large numbers of drift bottles in a given area, and using those returned to determine residual flow throughout the area. The path of drift inferred from a large number of recoveries, when considered with other parameters, can give a good indication of surface circulation.

RELEASE PROGRAM AND BOTTLE RETURNS

Release Network

A network of 14 stations was established in January 1957 and was covered repeatedly during a 2-year period (Fig. 1). At each station, in addition to releasing 6 drift bottles, salinity samples and temperature observations were taken at serial depths (Forgeron, MS, 1959) and plankton hauls (Legaré and Maclellan, 1960) were made. In the summer of 1957, the release network was increased to include 35 release points and as many as 56 release points were used for a few cruises. During January to March, 1957, only one cruise per month was carried out; from April 1957 until December 1958 the program consisted of two and occasionally three cruises per month. During the winter months only one semi-monthly cruise covered the same network as the one in summer, whereas the other cruise covered a modified network where the program consisted only of drift-bottle releases, surface sampling and surface temperature observations.

During the 2-year period altogether 48 cruises were carried out. Each cruise took approximately 4 days to complete, but the time varied from 2 to 15 days, depending on weather conditions.

In all, 8,430 bottles were released in the Quoddy Region; 2,391 in Passamaquoddy Bay, 564 in Cobscook Bay, 282 in the St. Croix estuary, 845 in Western and Head Harbour Passages, 281 in Letite Passage, 1,098 in Grand Manan Channel and 2,969 in the remaining portion of the outer Quoddy Region. A summary of bottle releases for each cruise is given in Table I.

In connection with a herring-tagging program (McKenzie and Tibbo, MS, 1959), 1,725 drift bottles were released, 48 at a time, at selected points throughout the Quoddy Region. Results of these experiments are not reported here, although the data have been used to assist, wherever possible, in deducing surface circulation in the Quoddy Region.

Two types of bottles (Fig. 2) were used for the drift-bottle project; the one used most extensively was an ordinary 8-ounce, clear-glass beverage bottle sealed with a rubber stopper and ballasted with sand so that it would be nearly submerged; the other was a 40-ounce glass jug, ballasted with sand and attached to a drag with 5 ft of wire. The drag was made from a 1-ft square of sheet metal cut and folded to have equal areas in three mutually perpendicular planes. Its purpose was to minimize the direct effect of wind and give a more realistic picture of the motion of surface waters.

Percentage Returns

For the 2-year period, a total of 2,074 bottles or 25% was recovered by February 1959. Table I gives the percentage of returns for each cruise after 10 days, 30 days, and overall. The percentage returns are high compared to returns from open-ocean experiments. From Table II it is evident that bottles released in confined areas such as Passamaquoddy Bay and Western and Head Harbour Passages resulted in a higher return, approximately 36% and 30% respectively,

TABLE I. Summary of drift bottles released and percentage of returns for each Quoddy Project and Betty Lou cruise.

Quoddy Project and Betty Lou (BL) Cruise No.	Date	Number released	Returns					
			After 10 days		After 30 days		Overall	
	1957		*No.*	%	*No.*	%	*No.*	%
1	10–25 Jan.	84	0	0.0	6	7.2	21	25.0
2	11–19 Feb.	84	7	8.3	14	16.7	27	32.2
3	7–13 Mar.	84	2	2.4	7	8.3	20	23.8
4	4–8 Apr.	84	9	10.7	15	17.9	21	25.0
5	15–18 Apr.	84	8	9.5	16	19.0	25	29.9
6	7–9 May	84	14	16.7	22	26.2	27	32.2
7	21–23 May	83	12	14.5	19	22.9	29	35.0
8	4–6 June	83	10	12.0	24	29.0	38	45.8
9	17–19 June	84	15	17.9	30	35.8	45	53.7
10	2–4 July	84	14	16.7	26	31.0	40	47.6
11	16–18 July	84	13	13.5	20	23.8	32	38.1
BL–2	22 July	12	2	16.7	6	50.0	8	66.7
12	July 30–Aug. 2	96	9	9.4	19	19.8	24	25.0
13	12–15 Aug.	210	11	5.2	34	36.2	63	30.0
14	27–29 Aug.	84	12	14.3	18	21.4	33	39.4
15	9–12 Sept.	210	8	3.8	23	10.9	43	20.4
16	23–26 Sept.	210	35	16.6	42	20.0	58	27.6
17	7–9 Oct.	210	25	11.9	45	21.4	68	32.4
18	21–24 Oct.	210	17	18.1	26	12.4	46	21.9
19	4–6 Nov.	246	27	11.0	53	21.5	72	29.2
20	19–22 Nov.	246	25	10.2	45	18.2	67	28.2
BL–3	2–4 Dec.	234	11	4.7	29	12.4	36	15.7
21	16–19 Dec.	210	25	11.9	38	18.0	52	24.8
	1958							
BL–4	7–8 Jan.	240	10	4.2	23	9.6	28	11.6
22	21–24 Jan.	210	26	10.8	32	15.2	43	20.5
BL–5	4–5 Feb.	240	2	0.8	8	3.3	21	8.8
23	17–20 Feb.	210	8	3.8	15	7.2	26	12.4
BL–6	3–4 Mar.	237	19	8.0	35	14.8	55	23.2
24	17–20 Mar.	210	25	11.9	34	16.2	55	23.0
25	Mar. 28–Apr. 8	204	19	9.3	24	11.8	31	15.2
26	14–17 Apr.	210	10	4.8	31	14.8	39	18.6
27	Apr. 28–May 1	210	12	5.7	19	9.0	43	20.4
28	12–14 May	210	17	8.1	34	16.1	60	28.3
29	26–28 May	210	14	6.7	35	16.7	56	26.6
30	9–12 June	210	15	7.1	34	16.1	65	30.9
31	23–26 June	210	17	8.1	33	15.7	51	24.3
32	7–10 July	210	16	7.6	40	19.0	64	30.5
33	21–23 July	210	22	10.5	40	19.0	59	28.1
34	4–7 Aug.	210	24	11.4	48	22.9	60	28.5
35	18–21 Aug.	210	21	10.0	40	19.0	56	26.6
36	2–5 Sept.	210	36	17.1	57	27.1	67	31.9
37	15–18 Sept.	210	47	22.9	55	26.2	65	30.9
38	Sept. 29–Oct. 2	209	11	5.2	21	10.1	26	12.4
39	14–16 Oct.	210	45	21.4	63	30.0	74	35.2
40	27–31 Oct.	210	24	11.4	33	15.7	40	19.0
41	15–17 Nov.	210	22	10.4	32	15.2	40	19.0
42	24–28 Nov.	210	14	6.7	27	12.9	38	18.0
43	9–11 Dec.	210	7	3.3	14	6.7	17	8.1
	Totals:	8,430	794	9.5	1,404	16.7	2,074	24.6

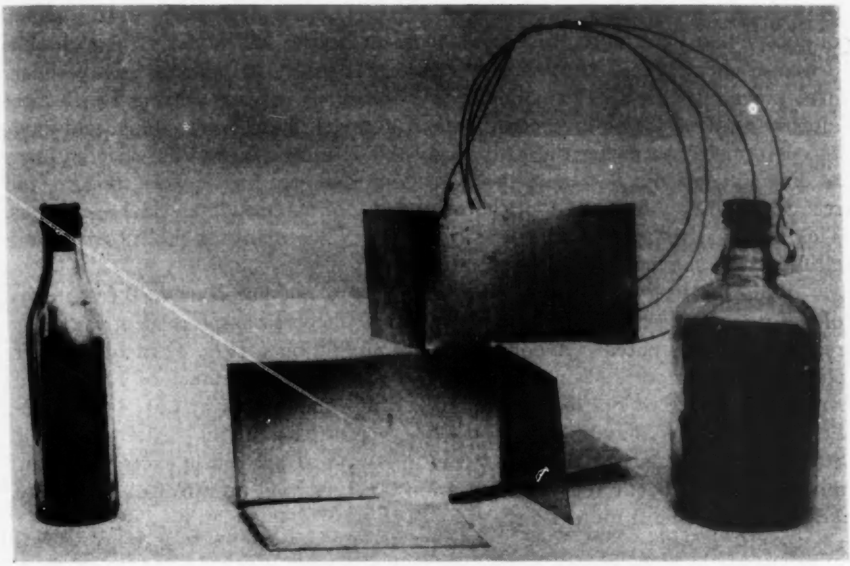


FIG. 2. Two types of drift bottles used on Quoddy Project cruises.

than those released in the outer Quoddy Region and Grand Manan Channel which yielded 16% and 11% respectively. Of all the bottles recovered, approximately 42% were released in Passamaquoddy Bay, 23% in outer Quoddy, 12% in Western and Head Harbour Passages, 8% in Cobscook Bay, 6% in Grand Manan Channel, 5% in St. Croix estuary, and 4% in Letite Passage (Table II).

TABLE II. Distribution of drift-bottle recoveries in relation to release areas.

	Areas of release								
Recovered	St. Croix River	Passama-quoddy Bay	Letite Passage	Western and Head Harbour Passages	Cobscook Bay	Outer Quoddy Region	Grand Manan Channel	Total	
								No.	%
St. Croix River	3	6	0	0	0	0	0	9	0.4
Passamaquoddy Bay	19	250	9	25	17	39	3	362	17.5
Letite Passage	18	215	28	37	17	85	9	409	19.8
Western and Head Harbour Pass.	40	241	21	104	61	98	33	598	28.6
Cobscook Bay	5	23	1	10	39	17	8	103	5.2
Outer Quoddy Region	22	94	23	40	19	160	18	376	18.1
Grand Manan Island	1	7	1	3	2	18	8	40	1.9
Nova Scotian coast	3	25	3	17	6	36	22	112	5.4
New England coast	0	6	4	5	5	26	16	62	3.0
Total*	111	867	90	241	166	479	117	2,071	100.0
Total released:	282	2,391	281	845	564	2,969	1,098	8,430	
Percent returned:	39	36	32	29	30	16	11		24.6

*3 bottles recovered in other areas not included.

Construction of assumed drift bottle paths is to a great extent intuitive and often open to question. In general, those of bottles whose net or straight line drift was shortest and most rapid were plotted first. Drifts progressively longer in distance and time were then plotted in conformity with each other and with those already drawn. Thus, the most indeterminate drifts were plotted last and made to conform to the pattern already evolved. However, in more restricted areas as Passamaquoddy Bay and the passages, the distance between release and recovery points is frequently of the same order of magnitude as tidal excursions. This makes it difficult to infer net circulation since many of the recoveries are all too easily subject to misinterpretation.

While bottles which travel most rapidly are not necessarily representative of the average speed of drift, a few examples of the possible speed occurring in the region should be noted. A bottle released at Station 6 (Fig. 1) at high water, travelled to Eastport, Maine, in 1 day, an approximate distance of 12 naut mi. Another, released at Station 13, was picked up 8 days later at Lat. 44°01′00″N, Long. 67°00′00″W, having travelled a distance of 64 naut mi. After release at Station 26, 3 bottles drifted to Eastport in 2 days at a speed in excess of 8 naut mi per day. A bottle released at Station 3 moved well up into Cobscook Bay, a distance of 14 naut mi in 1 day.

OTHER OBSERVATIONS

In conjunction with the drift-bottle program, temperature and salinity measurements (Forgeron, MS, 1959) were taken and plankton tows (Legaré and Maclellan, 1960) were made throughout the region. Electromagnetic measurements (Trites and MacGregor, MS, 1959) of tidal transports through the passages were made. Current measurements were taken over a tidal cycle from an anchored ship at some 60 locations (Forrester, MS, 1959). Radar-reflector-mounted drift poles were tracked and wind speed and direction monitored. Use was made of these observations wherever possible, to assist in establishing the most probable pattern of drift.

Radar-tracked Drift Poles

Part of the current measurement program involved use of radar-reflector-mounted drift poles which could be released in a pattern and tracked by means of radar. The technique was similar to that employed by Broc (1953) off the coast of Nice in France.

The shaft of the poles used in the present survey consisted of a piece of wood 2 × 4 in × 12 ft. On the upper end, a radar reflector consisting of either a 28-in stack of $4\frac{1}{4}$-in tetrahedrons or a single 14-in tetrahedron was attached. Steel floats were fastened 5 ft from the reflector. On the lower end of the pole, a drogue with 2 × 3-ft metal vanes was attached to reduce the direct effect of wind. To give the poles a large righting-moment, a concrete weight was attached below the drogue.

During 1957 and 1958, 5 series of drift-pole observations were carried out in Passamaquoddy Bay, 2 in Grand Manan Channel, 5 in the outer Quoddy Region between Deer Island and The Wolves and 1 in Western Passage. In general, an attempt was made to track the poles over the tidal cycle of 12.4 hr. Frequently this proved impossible because of poles stranding on shore or moving beyond range, or because of sea surface conditions and radar breakdowns. On other occasions, lost poles that were recovered at a later date provided useful information.

Grand Manan Channel experiments indicated a net drift northerly from 2½ to 3 naut mi per tidal cycle. Poles released between Head Harbour and Mascabin Point indicated a non-tidal drift 2 to 3 naut mi southwestward then northeastward. In Passamaquoddy Bay, the pattern of drift was complicated. Wind direction, and wind speed when it exceeded 10 mph, exerted a dominant influence on the drift of poles. Overall results suggested the existence of more than one eddy within the bay. One was a counter-clockwise movement in the eastern side of the bay fed in part by Letite Passage. Its westward boundary, although not well defined, was in the general vicinity of the line joining St. Andrews Point to Davidson Head on Deer Island (Fig. 1). A second eddy was located on the western side of the bay and fed in part by Western Passage. It moved in a counter-clockwise direction along the coasts of Maine and Deer Island as far as Davidson Head (Fig. 1). This eddy appeared elongated in the north–south direction but was not as marked as the eastern one. In both eddies, non-tidal drift did not exceed 2 naut mi per tidal cycle.

Wind Speed and Direction at Point Lepreau, N.B.

An anemometer was operated at Point Lepreau from January 1922 to December 1945 inclusive. It was reinstalled at the end of July 1957 as part of the program of observations in the Quoddy Region. Another instrument was installed by the Meteorological Service in June 1957 at the marine radio station near Saint John, N.B. Locations of these stations are shown in Fig. 1. Wind observations were also made in the Bay of Fundy region, at Saint John airport, N.B., at Lurcher Lightship (off Yarmouth, N.S.), and at Eastport, Maine. Data from Point Lepreau were analyzed on daily, 10-day, and monthly bases. Results for the Quoddy Region indicate a close relation between the course of drift bottles and wind direction. A 10-mph wind is enough to alter the course of a drift bottle. Further evidence of this relation will be given later in the study of patterns of drift-bottle movement.

The prevailing wind direction at Point Lepreau is from the southwest in summer, with a mileage of 7,000 to 8,000 per month. In winter, the wind blows from the west and northwest with a monthly mileage between 13,000 and 15,000. Figure 3 shows the 10-day average resultant of wind speed and direction at Point Lepreau and at Saint John, and a monthly average resultant of wind speed and direction at Point Lepreau for the period 1922 to 1945.

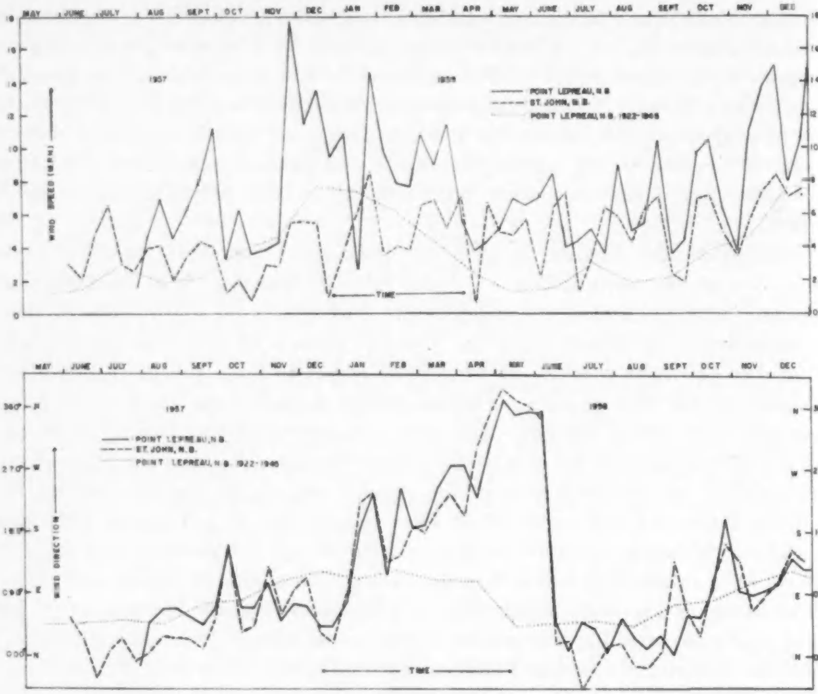


FIG. 3. Average resultant of wind speed and direction at two stations in the Bay of Fundy.

INTERPRETATION AND DISCUSSION OF RESULTS

Surface Circulation as Indicated by Drift-bottle Returns for Each Month During 1957 and 1958

In analyzing drift-bottle returns, the first step consisted of plotting the returns from each set of releases. While there were many differences in results on a localized scale, the broad features generally remained similar over most of a month and hence results could be conveniently plotted on a monthly basis. In addition, each plot included a graph showing resultant wind for each month on a 10-day basis. Observations from Saint John (Fig. 1) were used for June and July 1957 and from Point Lepreau for the period August 1957 to December 1958 inclusive. Wind vectors for these stations are considered representative of the wind pattern over most of the area. For conciseness only 2 of the 24 monthly plots have been illustrated (Fig. 4 and 5). These may be considered as giving basically the range of patterns of recovered bottles.

For the most part, conclusions to be drawn from inferred monthly patterns of drift were self-evident, but particular care was necessary in interpreting flow

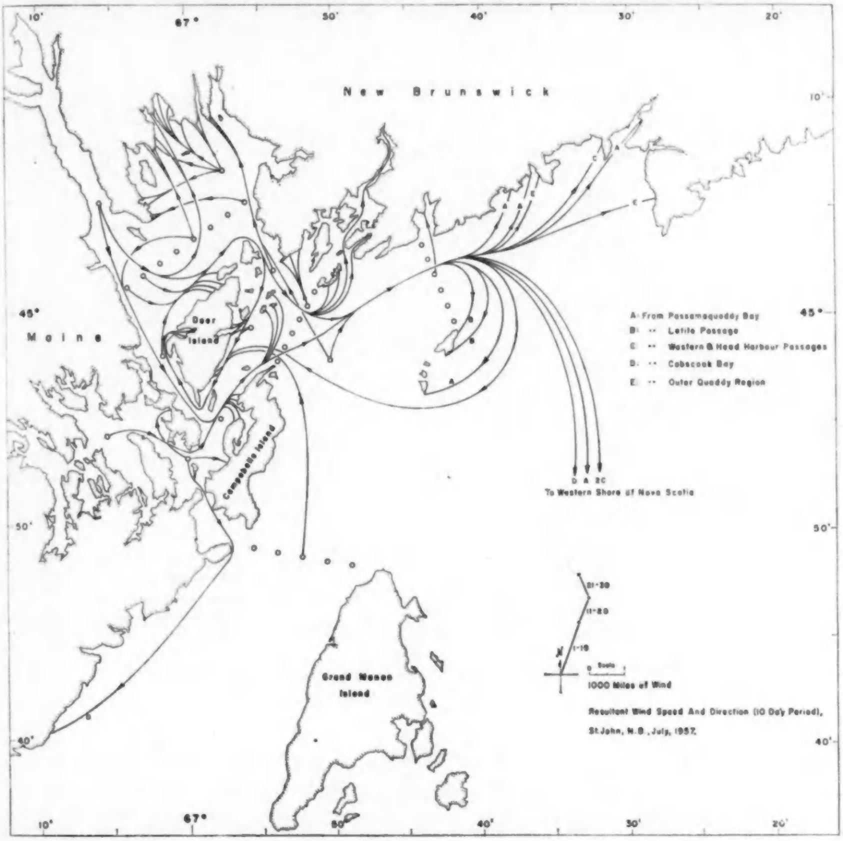


FIG. 4. Inferred pattern of drift bottle movement, and resultant wind speed and direction, July 1957.

through the passages. Results of other investigations indicated that usually a net inflow occurs through Letite Passage. Analysis of drift-bottle recoveries nevertheless led to a different conclusion, namely, a variable flow. However, the pattern of drift-bottle returns is subject to some misinterpretation with respect to residual flow. A bottle released at Station 5 (Fig. 1) at high water will have a high probability of escaping through Letite Passage on the ebb tide, whereas a bottle released outside the passage at Station 4 at low water may move on the flooding tide into Head Harbour Passage, or northeastward, or into Passamaquoddy Bay through Letite Passage. The probability of bottles moving directly into Passamaquoddy Bay is therefore less than that of bottles moving directly out of the bay. Thus, while more bottles escaped outward through Letite Passage than moved inward through it, the residual flow was not necessarily in the same

FIG. 5. Inferred pattern of drift bottle movement, and resultant wind speed and direction, January 1958.

direction as the apparent bottle motion. A somewhat similar phenomenon is to be expected for Western Passage.

General Pattern of Surface Circulation and Seasonal Variations

Dominant features of the monthly charts were combined to show seasonal patterns of drift (Fig. 7–10). Since certain features persisted throughout 1957 and 1958, a general pattern of surface circulation was constructed to include these features (Fig. 6). The results obtained suggest a counter-clockwise residual flow in Passamaquoddy Bay, an outflow in St. Croix estuary and Western Passage, and a variable flow in Letite Passage. Flow in Head Harbour Passage consists of a major outward movement on the Campobello Island side, and a minor inward movement along the southeastern side of Deer Island as far as Deer Island Point (Fig. 1).

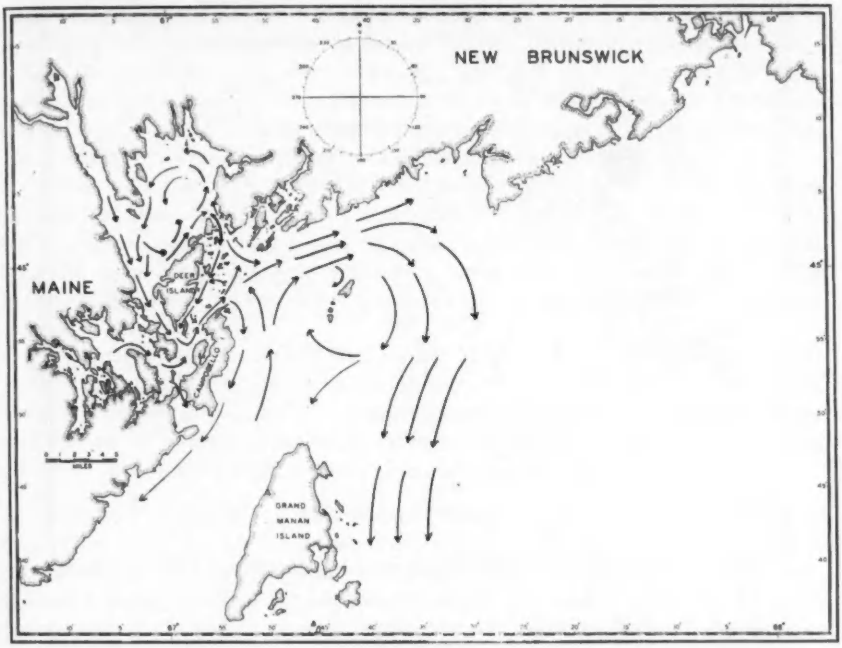


FIG. 6. General surface circulation in Quoddy Region as indicated by drift bottles for 1957 and 1958.

Residual flow in Cobscook Bay and Lubec Narrows is generally outward.

In the outer Quoddy Region, residual flow is eastward along the New Brunswick shore, swinging southward before Point Lepreau then southwestward around The Wolves in a clockwise direction to the eastern side of Grand Manan Island, and across the Bay of Fundy to Nova Scotia or along the coast of Maine.

Recoveries of drift bottles launched in Grand Manan Channel (Stations 22–25) suggest a residual flow which moves northward and joins the eastward drift along the New Brunswick shore. Part of this northward drift moves into Head Harbour Passage along the Deer Island side. A southwest drift moving parallel to the coast of Campobello Island and the coast of Maine is evident only during certain times of the year. The Wolves are at the centre of a usually apparent clockwise circulation.

WINTER (Fig. 7a, b)— Drift-bottle recoveries for the winters of 1957 and 1958 were 27% and 19% respectively. Since in the winter of 1957 only 3 cruises were carried out and 14 stations covered in the release network, the actual number of bottles returned was much smaller during the winter of 1957 than that of 1958 and gave only a limited indication of surface circulation for the winter season. In those two winters there was an apparent dominant flow outward through both Letite and Western Passages. There was no evidence of a

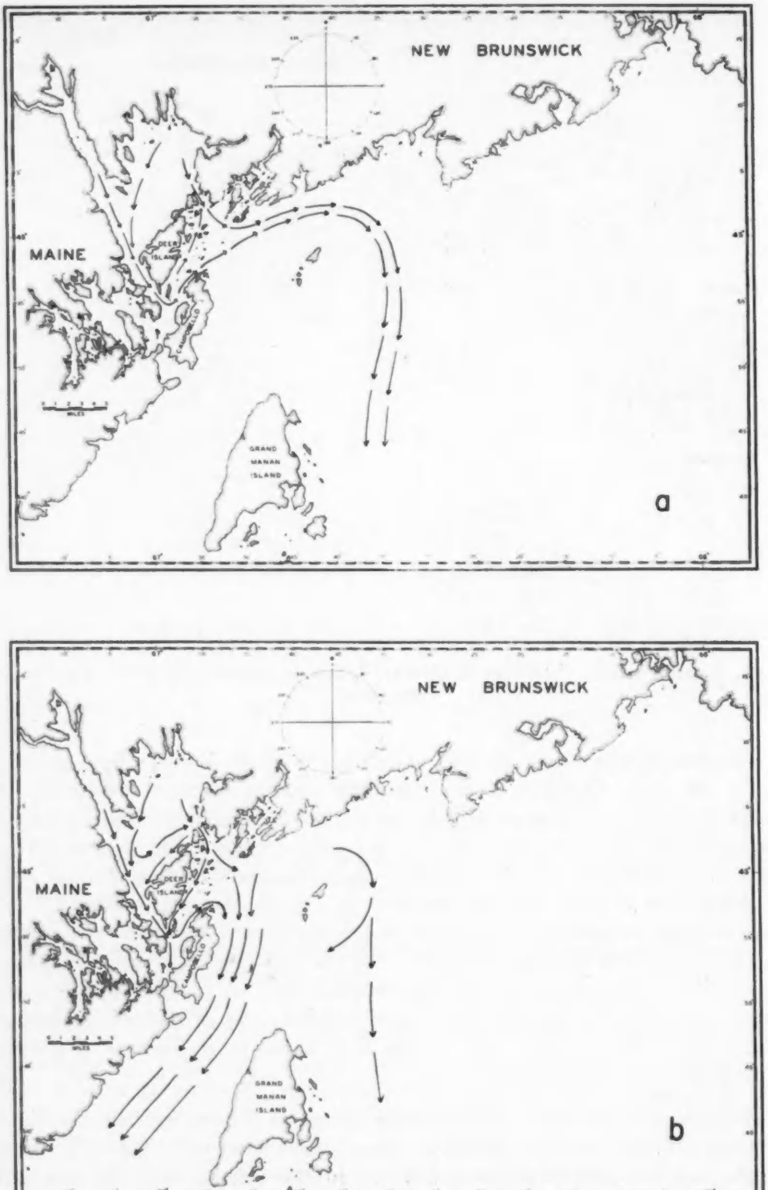


Fig. 7. Seasonal pattern of surface circulation as indicated by drift bottles. (a) Winter 1957. (b) Winter 1958.

counter-clockwise circulation in Passamaquoddy Bay. The 1957 recoveries gave no information concerning flow in Grand Manan Channel, whereas in 1958 a marked southwesterly flow was indicated. The flow was interpreted as being eastward between The Wolves and the mainland in conformity with the general pattern, but there was little conclusive evidence to support this. A residual flow outward between The Wolves and Grand Manan could have existed.

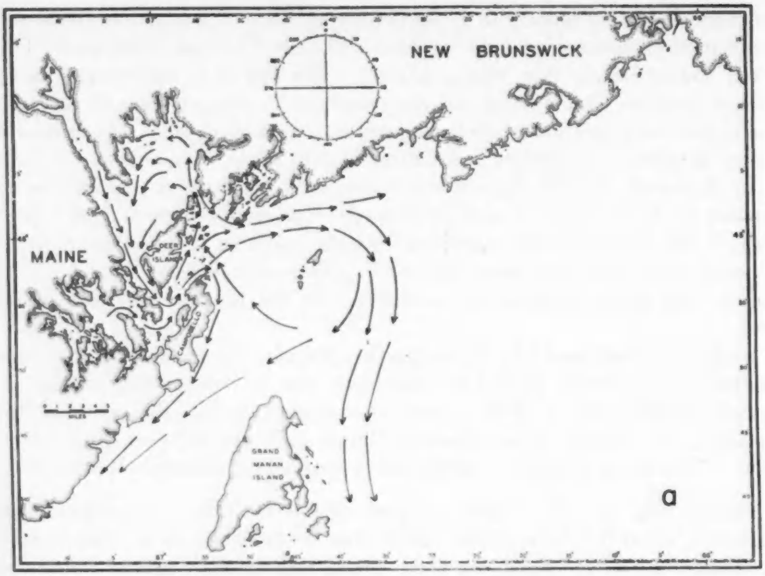
In the winter of 1958 there was a particularly high recovery of bottles along the coast of New England and a relatively low recovery from Nova Scotian shores. Only 2 bottles were recovered from the northern part of Passamaquoddy Bay, and none from the New Brunswick shore east of Bliss Island. During January 1958 many bottles were recovered on the northwestern side of Deer Island.

In the more confined area of the Quoddy Region, the wind, which had mostly a northerly component, played an important role in determining surface drift. However, particularly in 1958, a marked movement along the coast of Maine appeared to be related to an unusually large discharge of fresh water into the system. This brought large dynamic forces into action (Bumpus, 1960).

Spring (Fig. 8a, b)— Two features that differ from the general pattern of drift are noted for 1957. First, there was no evidence of an inward flow in Head Harbour Passage along the Deer Island side; second, several bottles were recovered along the New England coast, which led to the inference of a flow southwestward along Campobello Island and the coast of Maine. A moderate number of bottles recovered from the northern shore of Passamaquoddy Bay gave evidence of a counter-clockwise circulation within the bay. In 1958 the features were similar to the general pattern of drift.

Summer (Fig. 9a, b)— Early in the summer of 1957 a number of bottles entered Passamaquoddy Bay through Letite Passage. Many of these released both inside and outside the bay found their way to the northern part of the bay. A prevailing southerly wind appeared to be largely responsible for this recovery pattern. In the latter part of the summer, relatively few recoveries were obtained from Passamaquoddy Bay, while a particularly large number were stranded in the region between Bliss Island and Beaver Harbour. In 1958 many bottles released between Beaver Harbour and The Wolves at Stations 26 to 30 were recovered in Letite and Head Harbour Passages. By considering the time factor, it was concluded that many of these bottles did not drift around The Wolves and thence into the passages, but rather moved southwest and then northwest between The Wolves and the mainland. A moderately high and persistent recovery was reported from the northern shore of Passamaquoddy Bay throughout the entire summer.

Autumn (Fig. 10a, b)— The recovery pattern inside Passamaquoddy Bay suggests that the cyclonic circulation prevalent in summer months has, in part, broken down by autumn. In the outer Quoddy Region, the pattern of drift appears similar to average conditions, although evidence of a fairly marked



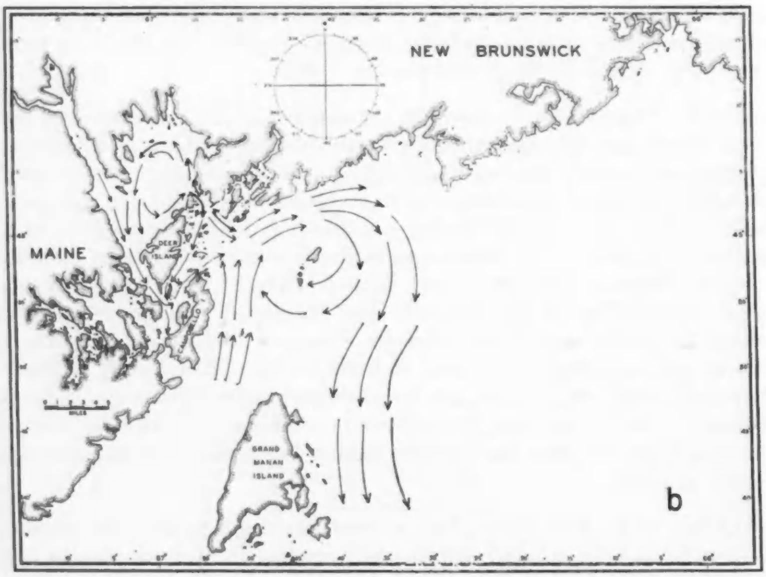


FIG. 8. Seasonal pattern of surface circulation as indicated by drift bottles. (a) Spring 1957. (b) Spring 1958.

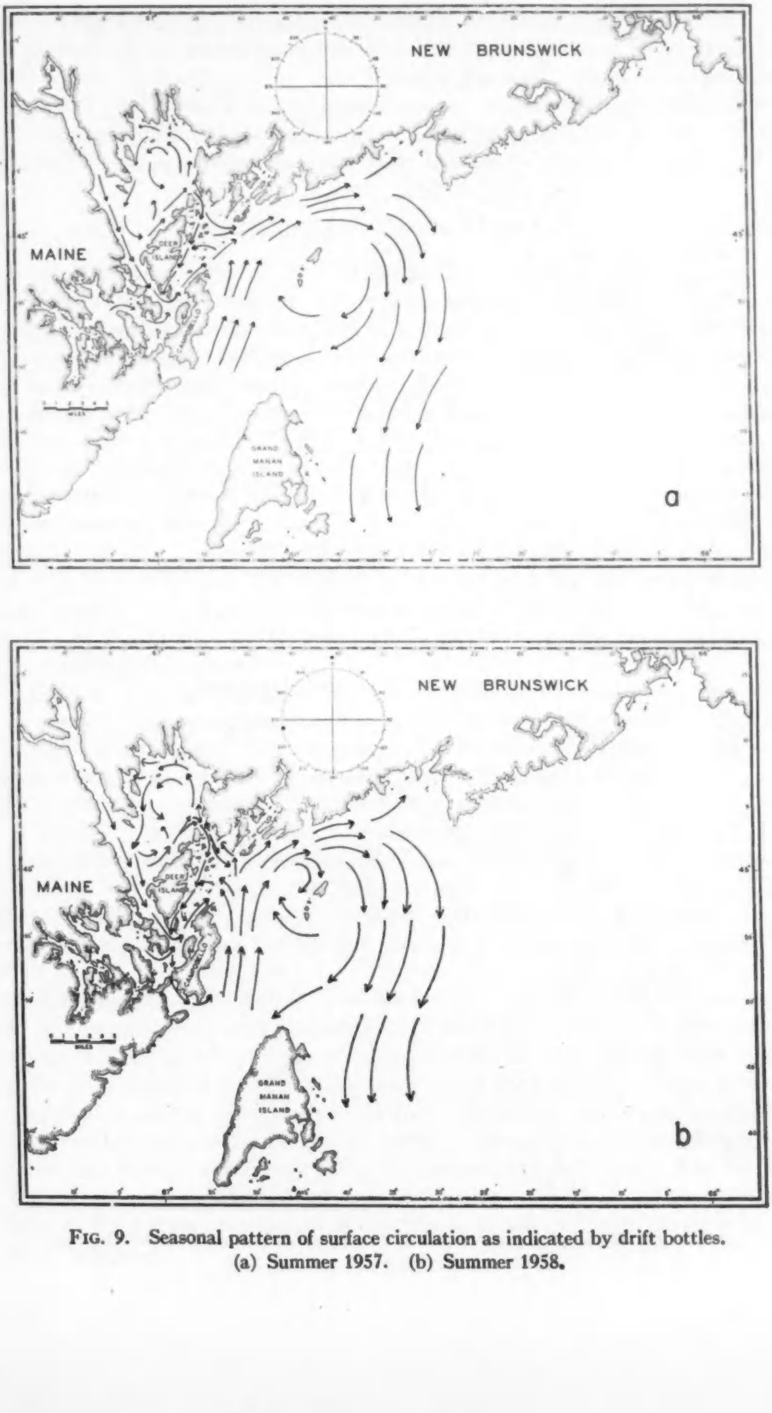


FIG. 9. Seasonal pattern of surface circulation as indicated by drift bottles. (a) Summer 1957. (b) Summer 1958.

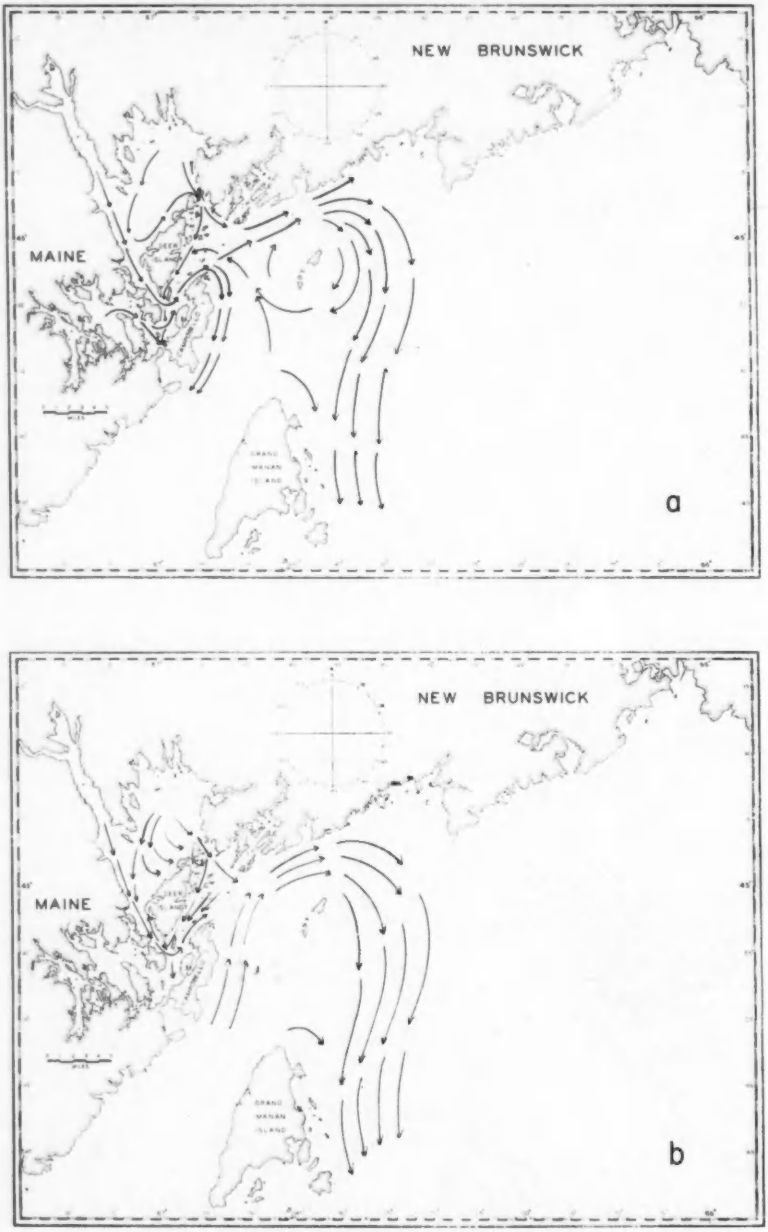


FIG. 10. Seasonal pattern of surface circulation as indicated by drift bottles. (a) Autumn 1957. (b) Autumn 1958.

flow soutwestward along Campobello Island in 1957 was absent in 1958. In 1958 a marked inflow was apparent on the Deer Island side of Head Harbour Passage, which persisted well up into Western Passage. There was virtually no evidence of any inflow through Letite Passage. Strong westerly winds drove many bottles ashore on the Passamaquoddy Bay side of Deer Island. There were practically no recoveries from the New Brunswick southern shore.

SUMMARY AND CONCLUSIONS

During 1957 and 1958, a total of 8,430 drift bottles was released in the Quoddy Region and approximately 25% were recovered. Returns were higher in enclosed areas, such as Passamaquoddy Bay where over 36% of the drift bottles launched were returned. In Grand Manan Channel, a relatively open area, only 11% of the bottles released were recovered. Approximately 29% of the recovered bottles stranded in Head Harbour and Western Passages, 20% in Letite Passage, 18% in the outer Quoddy Region, 17.5% in Passamaquoddy Bay, 5% in Nova Scotia, 5% in Cobscook Bay, 3% in New England, 2% in Grand Manan, and 0.4% in the St. Croix estuary (Table II). Bottles released in Passamaquoddy Bay (2,391) represented 28% of the total released while recovery constituted 42% of the total returned. In the outer Quoddy Region, the total release (2,969) represented 36% while only 16% were returned. Except for a few bottles found afloat off Cape Spencer, N.B., no recoveries were reported along the northwestern shore of the Bay of Fundy east of Point Lepreau. No bottles were recovered on the Atlantic coast of Nova Scotia.

Drift-bottle recoveries suggest that on the average there is a counter-clockwise circulation in Passamaquoddy Bay, a variable flow through Letite Passage, and an outflow through Western Passage. In Head Harbour Passage the flow is inward along Deer Island and outward along Campobello Island.

On the whole, wind action is very effective in determining the course of the drift of bottles. In general, winds from the south and southwest (summer) tend to confine surface waters to Passamaquoddy Bay, while winds from the north and west (winter) remove surface waters from the bay.

In Cobscook Bay the general pattern of drift was outward although it was not uncommon to find that bottles had penetrated well up into the head of this bay.

In the outer Quoddy Region, non-tidal drift is usually southerly along the coasts of Campobello Island and Maine. This drift was particularly evident during the winter of 1958, when a large number of drift bottles were found along the New England coast. There is evidence that on the average a clockwise circulation occurs around The Wolves. However, there are insufficient data to prove or disprove this for winter months. In general, it is concluded that surface waters leaving the Quoddy Region move outward between The Wolves and Point Lepreau, southward off the eastern side of Grand Manan Island, and thence either across the mouth of the Bay of Fundy to Nova Scotia or along the coast of Maine.

ACKNOWLEDGMENTS

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Studies on the Life-History of the Ascarid *Porrocaecum decipiens* in the Bras d'Or Lakes, Nova Scotia, Canada[1]

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ABSTRACT

Larvae of the parasitic ascarid (*Porrocaecum decipiens*) occurred commonly in the musculature and viscera of Atlantic cod (*Gadus morhua*) in the Bras d'Or Lakes. They were also present in the musculature of nine other species of teleosts and probably also in the viscera of skates (*Raja* sp.). Most larvae were longer than 20 mm. None was shorter than 10 mm, a fact which suggested the existence of some earlier intermediate host, probably an invertebrate. More than 8,000 mysids, an important food of fishes when they first become infected, were examined for nematodes. Although 110 nematodes were found, only one certainly and four dubiously appeared to be *Porrocaecum*. The definitive hosts were the harbour seal (*Phoca vitulina*) and the grey seal (*Halichoerus grypus*). The distribution of seals coincided with local variations in the incidence of the parasite in cod.

INTRODUCTION

In 1946 an investigation was begun of a nematode, *Porrocaecum decipiens* (Krabbe, 1878), also known as *Terranova decipiens* (Leiper and Atkinson, 1914), and, more recently, as *Phocanema decipiens* (Myers, 1959). It occurs commonly in the fillets of Atlantic cod in Canadian east-coast waters. In 1947 Dr Carl Medcof of the Biological Station, St. Andrews, N.B., told us that cod in Whycocomagh Bay (Fig. 1) were much less heavily infected with nematodes than cod from elsewhere in the Bras d'Or Lakes, Cape Breton Island, N.S. Reconnaissances of this area in 1947 and 1948 confirmed Dr Medcof's report. They further revealed that large numbers of small, young cod could be readily caught in the area. The Bras d'Or Lakes thus appeared to be an ideal locality in which to study the life-history of the parasite. Accordingly, a more intensive investigation was begun in 1949 and continued throughout the following three years. Further studies, more restricted in nature, were carried on in 1956 and 1958.

METHODS AND MATERIALS

Three localities were finally selected for intensive study: Baddeck Bay, Kempt Head and Whycocomagh Bay. These localities were selected because preliminary studies showed that the parasite was common in cod from Baddeck Bay and Kempt Head but scarce in Whycocomagh Bay. Baddeck Bay and Kempt Head represented shallow and deep areas respectively. Most of the fishing in Baddeck Bay was done at depths of about 15 to 20 m and in the Kempt

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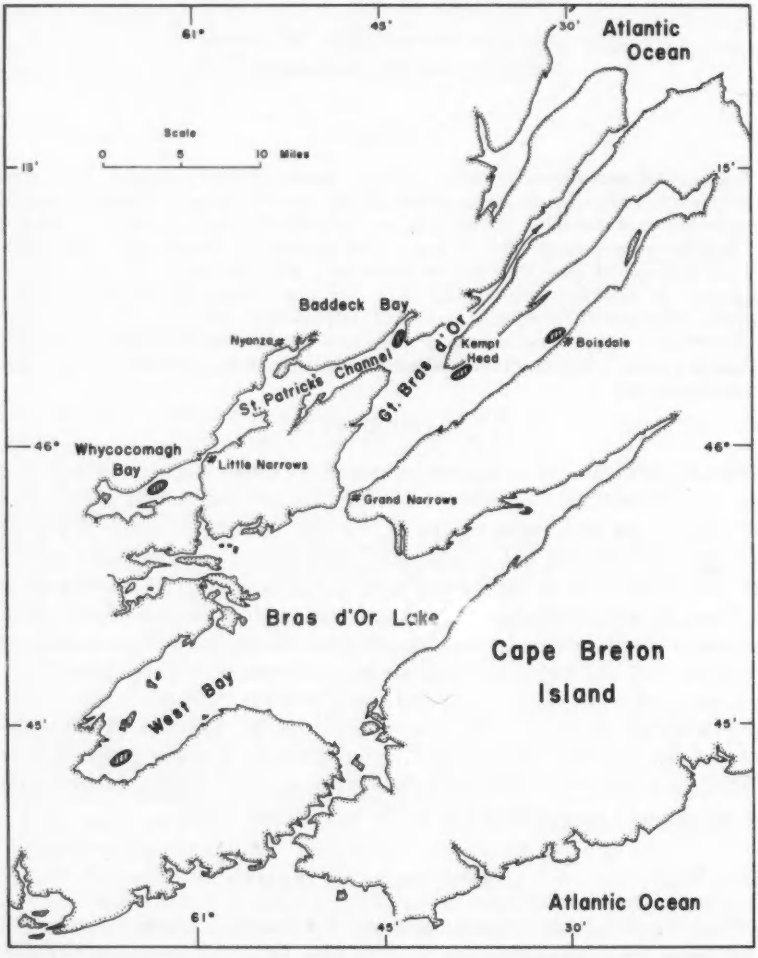

FIG. 1. Map of the Bras d'Or Lakes, Cape Breton Island, N.S., showing places mentioned in the text. Principal collections came from the hatched areas.

Head area at depths of 60 to 80 m. Whycocomagh Bay was intermediate in depth between the other areas. Smaller collections of cod were made near Boisdale, in West Bay, and in St. Patrick's Channel as far west as Nyanza. Samples from these areas, as well as smaller samples from other localities, were intended to provide information about the distribution of the parasite throughout the entire area.

The incidence of nematodes in the fillets of about 2,500 cod was determined by a method essentially similar to that described by Scott and Martin (1959). The incidence in 1950, 1951 and 1952 was determined in each year by different observers. No estimate of personal bias on the part of each observer could be obtained, Accordingly, the results of each year have not been compared, except very generally. For each cod examined, the fork length to the nearest centimetre and the age as inferred from examination of otoliths were recorded. Determinations of age were originally made by one of several technicians or by one author. Subsequently, at least 20% of the otoliths in each sample were re-examined by Scott. Where differences between original and subsequent observations occurred frequently, the entire sample was re-examined. In this way reasonable uniformity in age determination was attained.

Fillets of fishes other than cod were occasionally examined for nematodes, but no attempt was made to determine the incidence of infection precisely.

More than 1,000 nematodes, ranging in length from 10 to 50 mm, were collected from the fillets of fishes, mostly cod, and preserved for later identification. Before preservation the lengths of 572 live nematodes from cod from Baddeck Bay were measured by Scott (1956). The lengths of an additional 116 nematodes preserved in formalin from cod from Kempt Head were also determined. These were measured by straightening and holding a nematode against a ruler graduated in millimetres. Samples of nematodes were also collected from the body cavity and from the digestive tract of cod.

More than 8,000 mysids were collected in 1958 from Kempt Head. They were examined to determine if any of the nematodes known to occur in mysids was *Porrocaecum*.

OBSERVATIONS

Identity of the Nematodes

About 1,000 nematodes recovered from the fillets of Atlantic cod and several other species of fishes were identified. All were larval stages of the genus *Porrocaecum*. Another genus of nematodes, *Anisakis*, occurs in cod fillets elsewhere in Canadian Atlantic waters (Templeman, Squires and Fleming, 1957; Scott and Martin, 1959). This genus, however, was not observed in cod from the Bras d'Or Lakes. Therefore, for all practical purposes, all larvae in cod muscle from this region are considered to be larval *Porrocaecum*. Evidence has been presented by Scott (1956) that these nematodes belong to a single species, *P. decipiens* (Krabbe).

Teleosts Hosts

Larval *Porrocaecum* were found in fillets of 10 fishes in the Bras d'Or Lakes:

Smelt, *Osmerus mordax* (Mitchill)
Mailed sculpin, *Triglops pingeli* Reinhardt
Shorthorn sculpin, *Myoxocephalus scorpius* (Linnaeus)
Longhorn sculpin, *Myoxocephalus octodecemspinosus* (Mitchill)
Sea raven, *Hemitripterus americanus* (Gmelin)
Eelpout, *Macrozoarces americanus* (Bloch and Schneider)
Atlantic cod, *Gadus morhua* Linnaeus
Greenland cod, *Gadus ogac* Richardson
Plaice, *Hippoglossoides platessoides* (Fabricus)
Yellowtail flounder, *Limanda ferruginea* (Storer)

Nematodes which were apparently *Porrocaecum* were found, usually tightly coiled, between the *serosa* and the *muscularis* or within the *muscularis* itself of the stomachs of skates (*Raja* sp.) taken in Baddeck Bay.

Distribution and Appearance of Larvae in Fish

Porrocaecum larvae occurred in the somatic musculature and the viscera of other fishes. In the musculature larvae were widely scattered between the nape and caudal peduncle. They were concentrated in the muscle adjacent to the body cavity and were less and less common in progressively more posterior regions. As those observations agree with those of Templeman, Squires and Fleming (1957), reference may be made to their account for further details. In the viscera, *Porrocaecum* larvae in company with other larval nematodes were often found in the liver, on the pyloric caeca, on mesenteries and attached to the tunica serosa of the digestive tract. Occasionally in large, heavily infected cod, knots of 30 or more nematodes were observed, bound together by connective tissue in the coelom near the posterior end of the rectum. Larval *Porrocaecum* were very rarely seen lying free in the body cavity of cod. *Porrocaecum* larvae were twice seen penetrating the peritoneum.

Porrocaecum larvae were found in 4 of the 156 cod stomachs examined. In each case the larvae were associated with recently ingested smelt or cod. No *Porrocaecum* were found in the lumen of the intestine or in the mucosa of the stomach or intestine.

Although the larvae were usually lying free and uncoiled or loosely coiled within muscle, they were frequently tightly coiled and enclosed in a capsule, presumably formed of connective tissue of the host. The appearance of the capsule varied considerably. In apparently early stages of encapsulation, the flattened ovoid capsule was white, soft and smooth. Larvae enclosed in such capsules appeared fully active when released. Capsules in later stages of encapsulation were brown or yellowish with rough, hard walls. Within the capsule the coils of the larva appeared to be joined together by strands of connective tissue. In many instances the larva showed signs of necrotic effects in that its capsule was rough and coarse. Finally, some capsules were dark brown with

irregular outlines; internally, traces of the larva could sometimes be seen but generally the capsule enclosed an amorphous mass of brown matter.

Encapsulated larvae were rarely found in cod less than 5 years of age or in smelt, which were usually 2 or 3 years old. In older cod, as well as in old plaice, many more encapsulated larvae were observed. In large, old cod there were sometimes concentrations of 40 to 50 larvae in the muscle of the anal region. These nematodes were usually in an advanced stage of encapsulation.

LENGTH AND GROWTH OF *Porrocaecum* IN COD

The lengths of living *Porrocaecum* larvae varied between 11 and 51 mm. Within this range, as Table I shows, about 95% were longer than 30 mm and

TABLE I. Mean total length, and length frequencies in 10-mm groups, of *Porrocaecum* larvae from the fillets of successive age-groups of cod from Baddeck Bay and Kempt Head, Bras d'Or Lakes, N.S. Larvae from Baddeck Bay were measured alive, those from Kempt Head after preservation in 10% formalin.

Length of larvae		Baddeck Bay							Kempt Head	
	Cod age:	I	II	III	IV	V	VI	>VI	I	II
	No.:	(4)	(4)	(25)	(14)	(12)	(8)	(12)	(10)	(30)
mm		*no.*	*no.*	*no.*	*no.*	*no.*	*no.*	*no.*	*no.*	*no.*
11–20		2	3	4	1	0	0	0	9	7
21–30		3	0	7	3	0	3	3	31	36
31–40		7	11	87	48	56	36	72	7	25
41–50		2	2	73	40	40	16	62	0	1
51–60		0	0	0	0	0	1	0	0	0
Mean, *mm*		32	33	38	40	40	37	40	26	29

slightly more than 40% exceeded 40 mm in length. In 1- and 2-year-old cod there were proportionately many more small nematodes (i.e., less than 31 mm long) than in the older groups. Nevertheless, even in the two youngest age-groups of cod most of the larvae were in the 31 to 40 mm group. The mean lengths of *Porrocaecum* from cod of age-groups I and II were appreciably less than those in the five older groups of cod. In the latter there was no apparent relation between mean length of nematodes and age of cod.

Because the sample of 1- and 2-year-old cod was small, a larger sample of cod of these ages was collected in 1958 from the Kempt Head area. The length frequencies of the preserved *Porrocaecum* found in these cod are recorded in Table I. These nematodes varied in lengths between 14 and 42 mm. As was the case in the sample from Baddeck Bay, the lengths of relatively few nematodes fell within the shortest length-group. The mean length of the nematodes in age-group II cod was 3 mm more than that in 1-year-old cod.

Templeman, Squires and Fleming (1957) found that of 1,013 *Porrocaecum* larvae measured by them only 6 were 20 mm or less in length and none was less than 15 mm long. Their observations, together with our data, indicate that larval

Porrocaecum are at least 10 mm, and probably much more, in length when they first enter cod fillets.

Porrocaecum larvae probably grow in length following their entry into cod muscle. The nematodes in our sample of 1-year-old cod (collected at an age of about 15 months) could have been in the fish no longer than this time. The wide variation in length of these nematodes is compatible with either the idea of entrance at a small and relatively uniform size followed by growth or with the idea of entry at sizes covering most of the length range. Since there were proportionately more nematodes in the longer groups in age-group II cod, it is a reasonable conclusion that this change in length distribution resulted from growth in length of the nematodes which had entered earliest. The period of growth must be short, relative to the potential length of life within the host, since there was no evidence of an increase in length of *Porrocaecum* in increasingly older groups of cod.

It is difficult to account for the absence of *Porrocaecum* of 11 to 20 mm in length from the three oldest groups of cod. Cod are apparently infected continuously throughout life; accordingly, small *Porrocaecum* should occur even in the oldest cod. Probably their apparent absence is attributable to our failure to perceive small nematodes in the large, thick fillets of old cod.

Incidence of *Porrocaecum* in Cod

The number of *Porrocaecum* per cod in Baddeck Bay, which was reasonably representative of most of the area, increased throughout the life of the cod. Table II shows that the mean number of nematodes per 1-year-old cod was 2.4, about 80% of these cod being infected. Thereafter the incidence and intensity of infection increased greatly; more than 95% of 2- and 3-year-old cod were

Table II. Number of *Porrocaecum* larvae in fillets of 13 age-groups of cod caught in Baddeck Bay in June 1949, and July 1950. The samples for each year have been combined.

Age-group	Number of cod	Av. fork length	Av. no. of larvae per fish (2 fillets)
yr	*no.*	*cm*	*no.*
I	110	23	2.4
II	81	31	10.3
III	59	37	8.7
IV	124	42	12.3
V	87	47	15.4
VI	52	52	27.7
VII	10	51	34.5
VIII	9	59	27.8
IX	24	60	40.0
X	6	59	57.7
XI	8	69	97.6
XII	2	79	173.0
XIII	1	83	330.0

infected, often to a remarkable extent. Several cod of these ages had more than 20 *Porrocaecum* in their fillets. Older cod were invariably infected, usually heavily. Some large cod had several hundred nematodes in the fillets in addition to large numbers in the viscera. The increase in the abundance of *Porrocaecum* with increasing age of the host was also noted in other localities in the Bras d'Or Lakes (Table III).

TABLE III. Variation in the average number of *Porrocaecum* per cod in several age-groups of cod from 6 localities in the Bras d'Or Lakes in 1950 and 1951. Only samples of 20 or more cod were considered.

	Age-group of cod				
	I	II	III	IV	V
Atlantic entrance to Great Bras d'Or					
1951	0.05	...	...	...	..
Kempt Head					
1950	5.1	8.5	...	14.1	16.8
1951	...	7.7	14.1	...	20.3
Baddeck Bay					
1950	2.8	10.6	...	13.3	15.8
1951	...	11.0	17.5	...	20.0
Boisdale					
1950	...	5.7	...	8.2	12.1
West Bay					
1950	...	4.0	...	11.4	15.4
Whycocomagh Bay					
1950	0.10	0.30	...	0.60	1.3
1951	0.10	0.25	0.39	...	1.5

Larval *Porrocaecum*, as attested to by their occurrence in cod, were widely distributed and common in most parts of the Bras d'Or Lakes (Table III). They were most abundant in the samples of cod from Baddeck Bay and Kempt Head. Cod from Boisdale and West Bay were less heavily infected. Samples (not recorded in Table IV) in the areas immediately north and south of Grand Narrows and from St. Patrick's Channel were also heavily infected, approximately to the same extent as those from Baddeck Bay and Kempt Head.

TABLE IV. Variation in the mean fork length (cm) of cod from 3 localities in the Bras d'Or Lakes in 1950, 1951 and 1952. Only samples of 10 or more fish were considered.

Age-group of cod	Baddeck Bay			Kempt Head			Whycocomagh Bay		
	1950	1951	1952	1950	1951	1952	1950	1951	1952
yr	*cm*	*cm*	*cm*	*cm*	*cm*	*cm*	*cm*	*cm*	*cm*
I	24.9	...	20.5	17.4	...	19.0	19.6	18.1	20.2
II	31.3	33.6	...	23.1	25.1	22.2	26.8	27.6	27.3
III	...	37.2	...	...	29.1	29.0	...	33.5	32.9
IV	42.6	...	...	32.8	...	32.3	39.4	...	37.5

Only two localities were found where *Porrocaecum* was relatively scarce in cod. Samples of fish from Whycocomagh Bay, despite the fact that this bay is only about 10 miles from the heavily infected area of St. Patrick's Channel, in all 5 years of study revealed very low incidences. For example, in 1950 and 1951, 1- and 2-year-old cod from Whycocomagh Bay averaged 0.10 and 0.30 nematodes respectively in their fillets, values less than 5% of those recorded for comparable age-groups from Baddeck Bay or Kempt Head. In Whycocomagh Bay only about 10 and 20% of 1- and 2-year-old cod respectively were infected. The abundance of nematodes in older age-groups from this area remained by far the lowest in the Bras d'Or Lakes. This is clearly indicated by the fact that in 1950 and 1951 an average of 3 nematodes were found in each 7-year-old cod from Whycocomagh Bay as compared with a mean of 35 nematodes per cod of the same age from Baddeck Bay (Table III). The other area of low incidence was near the Atlantic entrance to the Great Bras d'Or. Here in 1951 only one nematode was found in a sample of 22 one-year-old cod. Small numbers of older cod from this area indicated that low incidences were characteristic of cod from this area.

We conclude from these data that local populations of young cod, each with a characteristic pattern of nematode incidence, were present in the Bras d'Or Lakes. Distinctive patterns of growth of cod from Baddeck Bay, Kempt Head and Whycocomagh Bay support this conclusion (Table IV).

Nematodes in Invertebrates

Eggs of *P. decipiens* hatch in sea water under experimental conditions (Scott, 1955). The eggs hatch into larvae enclosed in a moulted cuticle from which the larvae are unable to free themselves. The larvae probably then enter a host in which the old cuticle is lost. The absence from young cod of small *Porrocaecum* less than 10 mm long indicates that a host preceding the teleost host is involved in the life cycle of the parasite. Cod, smelt and mailed sculpin first become infected at a size when they were found by Black to be feeding almost exclusively on invertebrates. Therefore, this first intermediate host is almost certainly an invertebrate.

Black in 1951 made an intensive study of the invertebrates in the diet of cod in the Bras d'Or Lakes. Mysids were the most common item of food found in the stomachs of cod of all ages from Baddeck Bay and Kempt Head. They were not important in the diet of cod from Whycocomagh Bay. This difference in diet evidently resulted from differences in the availability of mysids in various areas. Collections of bottom-dwelling animals showed an abundance of mysids at Baddeck Bay and Kempt Head, but a scarcity at Whycocomagh Bay. Mysids were also important in the diet of other species of infected fish.

Black found in 1951 and 1952 that some mysids were infected with larval nematodes. Less than 20 specimens of these nematodes were available for identification. None appeared to be *Porrocaecum* and all that could be identified were *Contracaecum* (Scott, 1957). The absence of *Porrocaecum* in this small

sample did not rule out the possibility that mysids might be a host for *Porrocaecum*. Accordingly, in 1958, further collections of mysids were made, principally in the vicinity of Kempt Head. These collections contained about 8,500 mysids and a few euphausiids and decapods.

Each crustacean was examined for nematodes. The examination consisted of the removal of the carapace and an inspection of the cephalothorax. The abdomen of each animal was examined but was fully dissected only in large specimens (longer than 3 cm).

One hundred and ten nematodes were found, 34 being free in the jars in which the collections had been preserved. Seventy-one nematodes in mysids were distributed as follows: 50 in *Neomysis americana*, 9 in *Mysis mixta*, 2 in *M. stenolepis*, 1 in *Erythrops erythrophthalma* and 9 in unidentified mysids. Four were found in the euphausiid *Thysanoessa raschi* and 1 in the decapod *Crago septemspinosus*. All the nematodes were larvae less than 15 mm long and all but 5 showed the generic characteristics of *Contracaecum*. The remainder were of particular interest since they were either *Porrocaecum* or *Anisakis*. It may be noteworthy that 4 of these nematodes came from *M. mixta* and *M. stenolepsis*, but none was definitely from *N. americana*. The fifth was in a mysid whose state of preservation was too poor to permit generic determination.

Each of the *Porrocaecum* or *Anisakis* was too small or too poorly preserved to allow examination by dissection. An intestinal caecum characteristic of the genus *Porrocaecum* was present in one and probably another nematode. No intestinal caecum was apparent in the remaining 3 nematodes, which could therefore be either *Anisakis* or else *Porrocaecum* in which the intestinal caecum had not yet been developed to a recognizable extent. There is slight evidence favouring the latter possibility.

TABLE V. Length (mm) of certain characters of larval *Porrocaecum* or *Anisakis* found in mysids from the Bras d'Or Lakes, and the ratio of oesophageal to ventrical length.

Specimen number	Total length	Oesophagus (O)	Ventriculus (V)	Intestinal caecum	Ratio: O/V
	mm	*mm*	*mm*	*mm*	%
2	4.3	0.66	0.39	. . .	168
52	4.6	0.81	0.56	?	146
64	4.7	0 62	0.45	0.16	138
23	5.5	0.70	0.41	. . .	171
3	8.5	1.0	0.56	0.08?	179

The percentage ratios of the length of the oesophagus to ventriculus (Table V) resemble those determined by Templeman, Squires and Fleming (1957) for *Porrocaecum* rather than those for *Anisakis*. These authors showed that this ratio was usually less than 80% for *Porrocaecum* but more than this for specimens lacking an intestinal caecum. Furthermore, unpublished studies by Scott on

Anisakis showed that in 75% of the specimens the oesophagus was more than twice as long as the ventriculus.

Two main points emerge from this examination of crustaceans. First, small nematodes which were probably *Porrocaecum* occurred in mysids in Bras d'Or Lakes. Secondly, euphausiids and decapods were also hosts of nematodes in this region.

Predators on Teleosts

The existence of local populations of small cod in the Bras d'Or Lakes indicates that all stages in the life cycle of *P. decipiens* are passed in this area. The incidence of the parasite was generally so high that its definitive host is probably a common predator on teleosts. Since no adult *Porrocaecum* were found in teleosts the definitive host must be a predator which is not another teleost. Three groups of such predators occur within the Bras d'Or Lakes: elasmobranchs, birds and marine mammals.

Of the elasmobranchs, sharks were rare. Only two specimens, both spiny dogfish, *Squalus acanthias*, were caught. Skates of several species (*Raja*) were on the other hand common, particularly in Baddeck Bay, and, although less abundant elsewhere, were widely distributed throughout the remainder of the Bras d'Or Lakes. No observations were made on the feeding habits of skates in our investigation. However, since skates are known to be predators on small teleosts in other regions, they probably behave similarly in the Bras d'Or Lakes. The stomachs and intestines of 31 skates from Baddeck Bay and Kempt Head were examined. Seven adult nematodes, probably *Eustoma* sp. were the only nematodes found.

Several species of fish-eating birds (cormorants, mergansers and gulls) were widely distributed in the spring and summer but none was common. The scarcity of fish-eating birds in the Bras d'Or Lakes made it unlikely that an extensive collection of ascarids from such birds could be made within the time available to us. Accordingly, no collection was made. This decision was reached in light of the knowledge that adult *P. decipiens* had not been found in collections of ascarids from the stomachs of double-crested cormorants (*Phalacrocorax auritus*) collected in Maine and in the Miramichi Estuary, New Brunswick, (Scott, 1956) or in the herring gull (*Larus argentatus*) in the Bay of Fundy (Harrington, 1939). These observations have been supported by the absence of adult *P. decipiens* from stomachs of double-crested cormorants from the Atlantic coast of Nova Scotia (Scott, unpublished data) and from several species of marine birds from the Magdalen Islands (Myers, 1959). Furthermore, the species occurring in the Bras d'Or Lakes are migratory and would be absent from the region for much of the year. It is unlikely therefore that birds were important predators on teleosts and consequently could not be important hosts of nematodes in fish.

Apart from a single record of a porpoise, the only marine mammals observed were two species of seals, the harbour seal, *Phoca vitulina*, and the grey seal,

Halichoerus grypus. None was seen in the summer, but several hundred seals were usually present in the area from late November until March. Although the seals spread out through most of the lakes, they were most common in the area between Baddeck Bay and Grand Narrows. They were rare in Whycocomagh Bay. As far as we could ascertain from conversations with inhabitants around Whycocomagh Bay, no large groups of seals entered the bay. Examination of the contents of the stomachs of 12 harbour and 8 grey seals collected in the Great Bras d'Or between November and March showed that the seals had been feeding extensively on fishes, particularly cod. Of greater interest was the presence of immature and adult *P. decipiens* in each of the 20 stomachs examined. The mean number of this ascarid per stomach was about 250 for harbour seals and about 1,500 for grey seals (for details, see Scott and Fisher, 1958). About 10% of the ascarids were mature. *P. decipiens* matures after about three weeks in the stomach of a seal (Scott, 1953). The preponderance of immature nematodes therefore indicates that most of the nematodes had entered the seals within the preceding three weeks, probably following the arrival of the seals in the Bras d'Or Lakes. The nematodes could have been derived from only one important source: infected teleosts in the Bras d'Or Lakes. This is conclusive evidence of the importance of seals as definitive hosts of the larval *Porrocaecum* in fish in this area.

DISCUSSION AND CONCLUSIONS

In summary, this investigation has elucidated certain aspects of the life-history of *P. decipiens* in the Bras d'Or Lakes. Here, larvae of this ascarid are common in the musculature of several species of teleosts. The absence of small larvae in teleosts suggests, however, that an earlier intermediate host is an invertebrate. The scarcity of *Porrocaecum* in the samples of mysids does not rule out the possibility that mysids are an important intermediate host. In the course of a year a cod would surely eat many more mysids than were examined and could thus acquire the observed levels of infection. Following entry into the muscle of cod by way of the digestive tract, the larvae apparently grow rapidly at first. The larvae may remain in the cod with little additional growth for several years during which they become gradually encapsulated. Whether these encapsulated larvae would be infective to a definitive host is unknown. In large, old cod many larvae ultimately die. The presence of cod and many adult *P. decipiens* in the stomachs of harbour and grey seals provides good evidence that seals are definitive hosts of the parasite. Eggs of the parasite are released into the sea in the faeces of seals. What happens next is uncertain. As has been stated earlier, eggs do hatch in sea water under experimental conditions; there is nothing to suggest that they do otherwise in the sea.

Local variations in the abundance of the parasite in cod coincided with variations in the abundance of other hosts throughout the Bras d'Or Lakes. In the areas of Baddeck Bay and Kempt Head the incidence of *Porrocaeucm* was high and seals were abundant. Conversely, in Whycocomagh Bay the incidence

of larval *Porrocaecum* in cod was low and seals were scarce. Moreover, if mysids are invertebrate hosts of *Porrocaecum* their abundance in Baddeck Bay and Kempt Head areas would favour the transmission of early stages of the parasite from seals to fish. On the other hand, the scarcity of mysids in Whycocomagh Bay would further reduce the chances, already low because of the scarcity of seals there, of the parasite becoming abundant.

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Age, Growth and Sexual Maturity of Cod (*Gadus morhua* L.) in the Newfoundland Area, 1947-1950[1]

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CONTENTS

ABSTRACT

Samples of cod were collected from fishing gears in the coastal areas of Newfoundland and Labrador and from research otter-trawlers on the neighbouring banks from 1947 to 1950. Collections for the most part were from early summer to early autumn. Ages were determined using otoliths. Calculations of growth were based on average lengths and weights of the different age-groups in the samples.

The growth rates of cod from various parts of the area were found to differ widely. Labrador cod had the slowest growth rate, much slower than cod from other parts of the area. Cod from the east coast of Newfoundland and the northeastern part of the Grand Bank were also slow-growing. Cod from the southwestern part of the Grand Bank had the fastest growth rate. Though cod from St. Pierre Bank and southwestern Newfoundland were fast-growing, also, they exhibited a somewhat slower growth rate than those from the southwestern part of the Grand Bank. Cod from the west coast of Newfoundland grew faster than cod from the east coast, but slower than those from southwestern Newfoundland.

Though differences in growth rate were small between the sexes, the females generally grew at a slightly faster rate.

The influence of differences in temperature and in food supply on the growth of cod in the area is discussed.

Comparable growth data for the area published by several investigators are discussed. It is suggested that differences in these data were the result of variation in sampling locality, different sampling gears, different combination of individual samples and differences in age estimation.

Both the size and age at which all fish were sexually mature varied throughout the area of investigation. Labrador cod matured at an earlier age and smaller size than cod from other parts of the area, whereas cod from the southwestern part of the Grand Bank generally matured at a later age and larger size than cod from other parts of the area. Cod from the east coast of Newfoundland, the northeastern part of the Grand Bank, St. Pierre Bank and the southwest and west coasts of Newfoundland were intermediate between cod from Labrador and the southwestern part of the Grand Bank in age and size at maturity, fish from the east coast generally maturing at an earlier age and smaller size than fish to the south on the Grand Bank and St. Pierre Bank and from the southwest and west coasts.

The age, growth and sexual maturity relationships of cod from various parts of the area,

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when analyzed in the light of tagging experiments, meristic studies, parasite studies and hydrographic information, suggest the existence of at least four relatively distinct divisions in the cod population of the area, between which there is only limited intermingling. These are the Labrador, the Newfoundland east coast, the southern Grand Bank and the Newfoundland west coast divisions, with areas such as St. Pierre Bank and the Strait of Belle Isle being mixing areas of cod from adjacent divisions.

INTRODUCTION

It is well known that there is no particular rate of growth or average size at a given age which will apply to the cod for all parts of its distribution. Environmental conditions have a marked effect on growth. It is no surprise, therefore, that in the area under consideration, extending from northern Labrador to the southern tip of the Grand Bank and from the west coast of Newfoundland to Flemish Cap (Fig. 1), observations of the lengths and weights of cod of comparable ages have revealed variations in the growth rate of fish from different fishing grounds. The present study is a preliminary one and covers the period from 1947 to 1950 inclusive.

From 1931 to 1935 a vigorous research program on the life history of the cod was carried on in the area by the Newfoundland Fisheries Research Commission (in 1935 known as the Division of Fishery Research, Department of Natural Resources). The work was wide in scope (Thompson, 1943) and only a brief portion of it could be devoted to age and growth studies.

Since that time other workers have undertaken brief studies on age and growth of cod from various parts of the Newfoundland area. Ancellin (1954) published results of observations on cod taken off Labrador and on the Grand Bank during two trips of the French oceanographic ship *Président Théodore Tissier* in 1951 and 1952. Rojo (1955) gathered samples of cod during a trip on a Spanish commercial fishing trawler on the southwestern part of the Grand Bank in March 1953. Figueras (1957) studied material collected during a trip of a Spanish commercial trawler on the northern part of the Grand Bank in June 1955. Ruivo (1957) used samples collected by observers on board Portuguese commercial trawlers during fishing operations off the northeast coast of Newfoundland, October and November 1955, and off Labrador, August to November 1956.

MATERIALS AND METHODS

Collection of Samples

The material in this paper formed part of data collected on cod from the coastal areas of Newfoundland and Labrador and from the neighbouring banks from 1947 to 1950. Collections for the most part were from early summer to early autumn.

Figure 1 shows the location of the collecting points, and Table I lists the localities and dates from which samples were taken. For the inshore sampling, localities were chosen on the coasts, each fairly widely separated from the next so

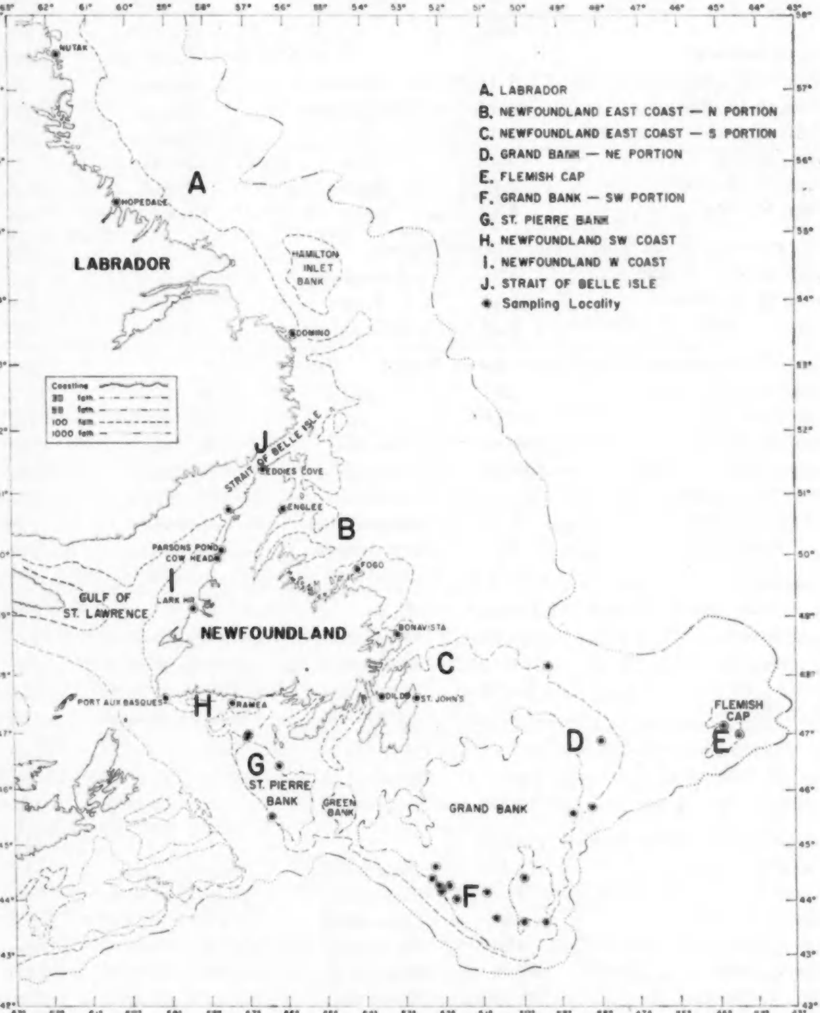

FIG. 1. Localities and positions from which the samples were taken. Refer to Table I for dates, depths and types of gear.

TABLE I. Dates, depths, types of gear and localities from which samples were taken.

Date	Depth	Gear	Locality	No. of fish
	fath			*no.*
A. LABRADOR				664
July 8–10, 1948	8–11	Trap	Domino	113
July 15–16, 1948	10–12	Trap, jigger	Domino	114
July 30, 1948	12–15	Trap	Hopedale	105
Aug. 6, 1948	12	Trap	Nutak	110
Aug. 11–12, 1948	2–15	Jigger	Nutak	111
Aug. 30, 1948	8–12	Jigger	Hopedale	111
B. NEWFOUNDLAND EAST COAST—NORTH PORTION				429
Aug. 26–Sept. 3, 1947	50	Linetrawl	Englee	210
June 27–29, 1949	11–16	Trap	Fogo	110
July 4–7, 1949	7–25	Trap, linetrawl	Fogo	109
C. NEWFOUNDLAND EAST COAST—SOUTH PORTION				828
June 30–July 2, 1948	18	Trap	St. John's	114
Aug. 3–5, 1948	9–18	Trap	St. John's	118
Sept. 27, 1948	40–50	Linetrawl	St. John's	46
Oct. 25–Nov. 1, 1948	30–70	Linetrawl	St. John's	110
Nov. 15–18, 1948	64–70	Linetrawl	St. John's	110
July 19–21, 1949	10–18	Trap, handline	Bonavista	110
July 26–28, 1949	15	Trap, handline	Bonavista	110
Aug. 11–12, 1949	30–35	Linetrawl	Dildo	110
D. GRAND BANK—NORTHEAST PORTION				459
June 9, 1948	60–75	Otter trawl	45°33′N, 48°43′W	112
July 27, 1948	105	Otter trawl	48°11′N, 49°18′W	116
July 13, 1949	95–108	Otter trawl	45°42′N, 48°11′W	111
June 16, 1950	70	Otter trawl	46°52′N, 48°00′W	120
E. FLEMISH CAP				242
July 11, 1950	100	Otter trawl	46°59′N, 44°26′W	123
July 11, 1950	90–104	Otter trawl	47°07′N, 44°52′W	119
F. GRAND BANK—SOUTHWEST PORTION				616
Apr. 12–24, 1947	45–51	Otter trawl	Southwest edge	120
May 4, 1947	31	Otter trawl	43°40′N, 50°00′W	58
May 16–17, 1947	36	Otter trawl	43°41′N, 50°43′W	73
May 29–30, 1947	47	Otter trawl	44°16′N, 51°54′W	68
May 16, 1948	35–36	Otter trawl	44°08′N, 50°57′W	81
Apr. 12, 1950	115–140	Otter trawl	43°36′N, 49°25′W	104
July 19, 1950	24–25	Otter trawl	44°25′N, 50°00′W	112
G. ST. PIERRE BANK				371
June 8, 1947	42	Otter trawl	45°24′N, 56°11′W	77
Apr. 24, 1948	96–104	Otter trawl	46°55′N, 57°00′W	108
July 3, 1948	65–95	Otter trawl	45°29′N, 56°28′W	78
Mar. 26, 1950	125–129	Otter trawl	46°59′N, 56°59′W	108

TABLE I—*Continued*

Date	Depth	Gear	Locality	No. of fish
	fath			*no.*
H. NEWFOUNDLAND SOUTHWEST COAST				346
June 2–6, 1949	15–25	Handline	Port-aux-Basques	121
June 8–9, 1949	10–15	Handline, linetrawl	Port-aux-Basques	114
June 16, 1949	20	Handline	Ramea Islands	111
I. NEWFOUNDLAND WEST COAST				572
July 31–Aug. 5, 1947	20–35	Handline, linetrawl	Lark Hr.	221
July 20–25, 1949	25	Handline	Cow Head	128
Aug. 5, 1949	18–23	Handline	Parsons Pond	115
Nov. 6, 1947	60	Otter trawl	50°47′N, 57°25′W	108
J. STRAIT OF BELLE ISLE				266
July 8, 1949	4	Trap	Eddies Cove	148
July 12, 1949	4	Trap	Eddies Cove	118

that the whole area could be covered; samples were collected from commercial gears. In each locality, over a 2- or 3-day period, samples of the unculled catches of inshore fishermen were taken, every effort being made to collect from several boats and from the various types of fishing gear used. It was hoped in this way to obtain as representative a sample of fish stocks in the area as is possible from commercial gears. These, of course, do not capture the youngest age-groups. Each kind of gear has a lower limit to the size of fish it will catch; traps and handlines catch fish of a smaller size than can usually be taken on line trawl (Templeman and Fleming, 1956). Near this lower limit, only the faster-growing, larger fish of the younger age-groups are caught. Because of this, the average sizes of these younger broods in the samples are probably somewhat higher than the true average in each case, and the age composition of the samples is affected.

The offshore samples were collected from the experimental otter-trawl catches of the research ship *Investigator II* operated by the Fisheries Research Board of Canada Biological Station, St. John's, Nfld. The offshore sampling localities were spaced, also, in order to collect from as wide an area as possible of Grand Bank, St. Pierre Bank and Flemish Gap. As was found for the inshore samples, the younger age-groups are absent, these being small enough to pass through the meshes of the net.

Fish were measured from the tip of the snout to the mid-fork of the tail and lengths were recorded to the nearest centimetre. Weights to the nearest tenth of a pound were taken of fish in the gutted condition with the gills removed.

In studying maturities males were considered immature when the testes were very narrow and string-like, with a narrow thin-walled vas deferens. Females were considered immature when the ovary was small and pinkish, the ovarian membrane thin and transparent, and the eggs not visible in the ovaries to the naked eye. Sexually maturing males with testes obviously developing and likely to spawn in the next spawning season, and females with ovarian eggs visible to the naked eye were included in the sexually mature group. Included

in this group, also, were the spent fish: the females with ovaries usually thick-walled and often containing residual eggs; the males with wide vasa deferentia, and often containing residual milt.

Determination of Age

The growth study is based upon the aging of about 4,800 cod. Ages were estimated using otoliths. A comparison of scales and otoliths at the beginning of the work showed that, especially for older fish, the outer zones of growth are much easier to distinguish on the otolith than on the scale. Other workers in the past have found otoliths to be superior to scales for aging cod, notably Rollefsen (1933), Dannevig (1933) and Hansen (1949). In Thompson's (1943) work in the area, ages were estimated using scales, but Ancellin (1954), Rojo (1955), Figueras (1957) and Ruivo (1957) have used otoliths.

Otoliths from Labrador and northeastern Newfoundland cod, because of a distinct difference between winter and summer zones of growth, were easier to interpret than those from cod of more southern localities of the area, where the contrast between the two types of zones is generally less distinct.

The actual determination of age from the otolith was made in a manner which is a simplification of a method used by Scandinavian investigators (Dannevig, 1933; Rollefsen, 1933). As Hansen (1949) found, it was not necessary after breaking an otolith to polish the broken ends in order to read the age, for the broken surfaces were generally smooth enough for the growth rings to be counted. The otolith was broken across the sulcus which is evident on the convex side and embedded in a block of black modelling clay, leaving only the broken surface visible. On this surface a drop of 1:1 solution of glycerine and water was placed and examination was made through a binocular microscope by reflected light, with magnification about 12 to 15.

To distinguish between the various age-groups, II-group, III-group, etc. have been used. The cod spawn in the area mostly in May and June. The collecting period was from April to November, but, for comparison of growth in length and weight, samples from April to September only were used. Fish which hatched from the spawning in May to June of one year were considered to be in the I-group for the duration of the collecting period (April to September) of the following year, and in the II-group during the collection period 2 years after hatching. Cod actually reach the age indicated by the numeral some time during the collection period and the I-group, for example, probably would contain fish about 10 to 16 months old.

Calculation of Growth

Growth in length was calculated on the basis of the average mid-fork lengths of the cod of the various age-groups in the samples. For some areas, where samples from more than one year were combined, each age-group will contain more than one year-class. Thus, in comparing the average lengths of a particular age-group from different areas, lengths of fish of more than one year-class are quite

often used. Since successive broods of fish in the same locality may exhibit differences in growth (Needler, 1930; Hansen, 1949) average lengths of age-groups which are made up of more than one year-class will yield results closer to the average growth for a locality.

Growth in weight is calculated on the basis of the average gutted weights of cod, with gills removed, from the various age-groups in the samples.

AGE AND GROWTH

Age Composition

Samples were taken from catches by different types of gears and in different years. Therefore, it was not found practicable to examine very closely the relative age compositions of the samples from different parts of the area.

Samples generally consisted of 10 to 15 age-groups, with few fish younger than the IV-group or older than the XV-group. Although there were differences in the relative strength of the year-classes in any one sample, in most cases so many of them were present and the degree of their differences so moderate that individual year-classes apparently did not play an important part in the control of abundance during the period of study. Rather does it seem that several moderately strong year-classes together predominated in the stock of a particular area at any one time. However, data gathered in later years and as yet unpublished indicate that year-class dominance does exist in cod stocks from the area.

Growth in Length

Growth rates of cod from various parts of the area were found to differ widely. Because of this there is a considerable variation in the average lengths of corresponding age-groups from different localities. In general, Labrador age-groups have the smallest average lengths and those from the southwestern Grand Bank have the largest average lengths.

Probably the ideal material for a comparison of growth rates in the area would be numbers of samples collected by research gear from the same localities at the same time each year. However, this ideal type of collection was not possible; the area was covered only once in 4 years (Table I), the number of fish sampled was not always the same, and the collection time varied. These limitations must be kept in mind when examining the results. Comparisons made suggest that their effect is not serious, but an adequate study of within-season and between-season variability in growth would require much more extensive collections.

Some variation is apparent between the growth of male and female cod in the area (Fig. 2). Differences are generally quite small in the younger age-groups and somewhat greater in the older age-groups. Though many irregularities exist in the curves, mainly because of the small amount of data, it is obvious that the females grow at a slightly faster rate than the males. Since the differences are relatively small, in the comparison of growth rates of cod from different parts of the area as shown in Figures 3 and 4 and Tables II and III, the data for both sexes have been combined.

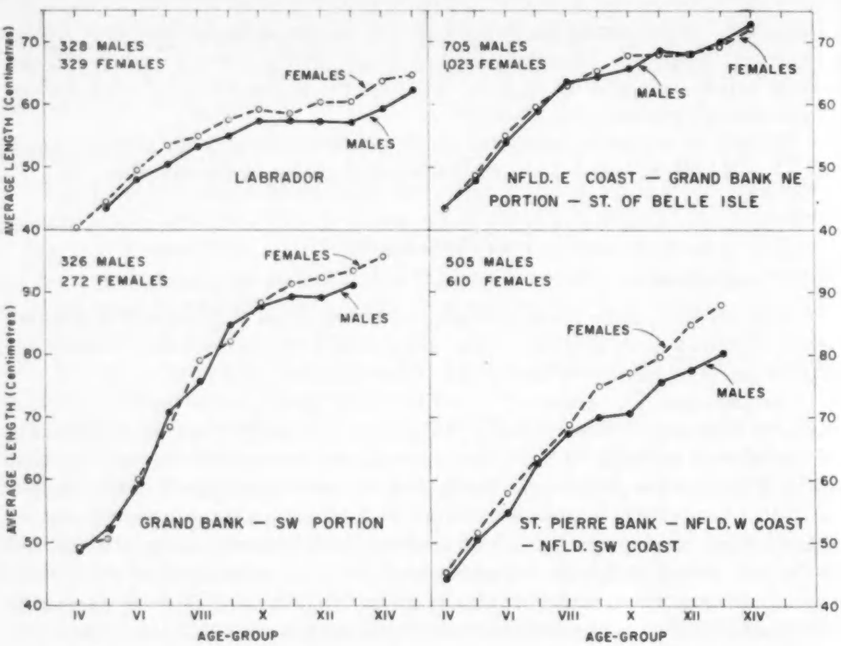

FIG. 2. A comparison of the average lengths (in centimetres) of male and female cod in each age-group from various regions, Labrador and Newfoundland, 1947–1950.

Table II shows the average lengths of the different age-groups in cod samples obtained from commercial fishing gears in various subdivisions of the Newfoundland–Labrador area. The subdivisions, as arranged from left to right in the table, are in geographical order proceeding from Labrador in the extreme north of the area, southward along the east coast of Newfoundland to the southern part of the Grand Bank, thence westward and northward into the Gulf of St. Lawrence as far as the Strait of Belle Isle (Fig. 1). The differences between the average lengths of corresponding age-groups are generally larger at the older ages than at the younger ones. Thus, the extreme difference recorded for the average length of the IV-groups, between Labrador and the southwestern part of the Grand Bank, is 7.9 cm; and for the XIV-groups, for the same localities, the difference is 33.6 cm.

In Figure 3 the results are presented graphically representing rates of growth of the cod from the different subdivisions. The curves are grouped in four lots to avoid confusion of too many lines on one graph and to compare rates of growth of cod from areas adjoining or close to one another.

There is a general increase in the rate of growth in length and weight of cod with decreasing latitude in the eastern part of the area, proceeding from Labrador to the southwestern portion of the Grand Bank (Fig. 3A). Although in cod from

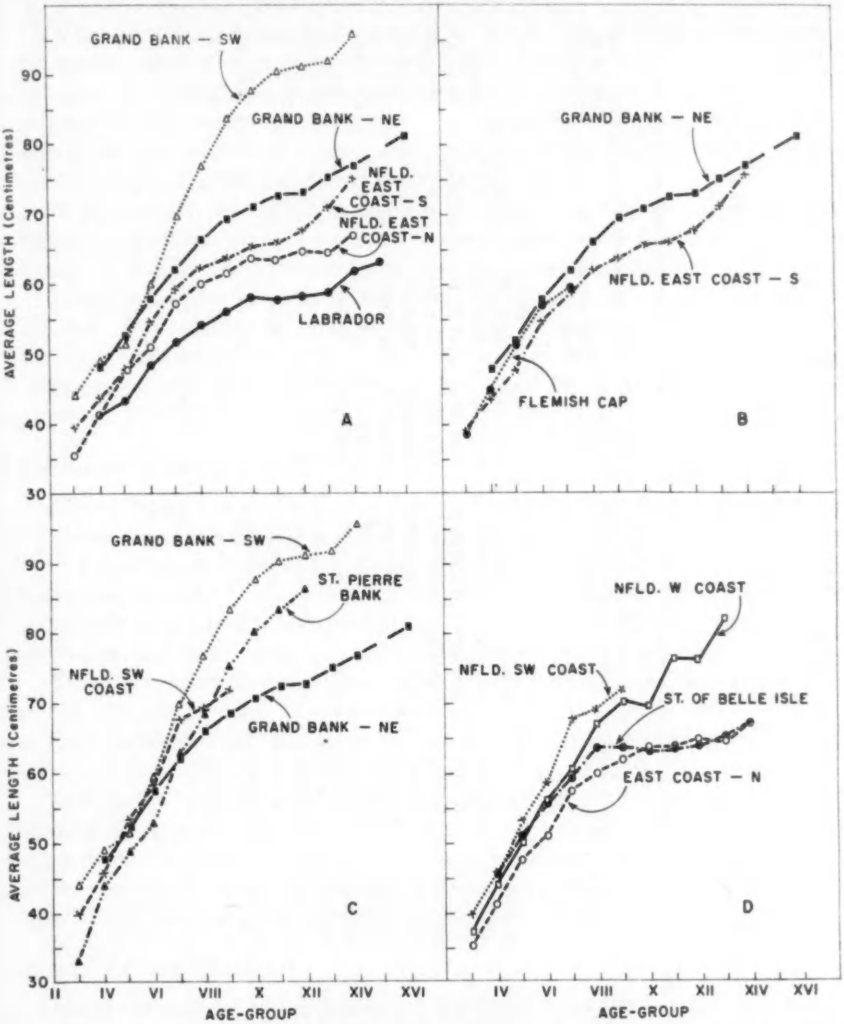

FIG. 3. Average lengths (in centimetres) of the different age-groups of cod from various localities, Labrador and Newfoundland, 1947–1950.

Labrador the growth rate is quite slow, in cod from the southwestern part of the Grand Bank growth is quite rapid.

In the sample from Flemish Cap only the younger age-groups are represented. The growth in length of these age-groups is intermediate between the growth rates of similar age-groups from the southern part of the east coast of Newfoundland and the northeastern Grand Bank (Fig. 3B).

TABLE II. Average fork length (in centimetres) of different age-groups of cod from various localities off Labrador and Newfoundland, 1947–1950. (Numbers of fish in parentheses.)

Age group	Labrador	E coast, N portion	E coast, S portion	Grand Bank, NE portion	Flemish Cap	Grand Bank, SW portion	St. Pierre Bank	SW coast	W coast	Strait of Belle Isle
	cm	*cm*	*cm*	*cm*	*cm*	*cm*	*cm*	*cm*	*cm*	*cm*
II	...	...	...	...	...	...	25.2(25)	24.0(26)	...	...
III	...	35.4(8)	39.3(8)	...	39.0(4)	44.0(2)	33.0(28)	39.9(42)	37.5(11)	...
IV	41.1(9)	41.4(34)	43.8(78)	48.0(3)	45.1(108)	49.0(95)	43.9(60)	45.9(35)	44.4(77)	45.8(8)
V	43.6(13)	47.7(38)	47.8(114)	52.7(12)	51.8(28)	51.6(58)	49.0(87)	53.5(110)	50.3(94)	51.3(32)
VI	48.8(126)	51.0(31)	54.8(69)	57.8(28)	57.1(68)	59.7(47)	52.8(28)	58.6(66)	56.3(64)	55.7(15)
VII	51.8(35)	57.2(60)	59.3(66)	62.2(44)	59.6(29)	69.8(88)	63.1(40)	68.0(27)	60.8(55)	59.5(23)
VIII	54.2(89)	60.1(34)	62.4(55)	66.2(45)	...	76.9(89)	68.8(24)	69.0(25)	67.3(27)	63.9(21)
IX	56.2(56)	61.7(60)	63.8(72)	69.5(68)	...	83.5(58)	75.8(19)	72.3(15)	70.4(21)	64.1(39)
X	58.4(58)	63.9(40)	65.8(49)	71.0(64)	...	87.6(55)	80.6(16)	72.8(8)	69.8(18)	63.5(21)
XI	57.8(86)	63.7(34)	66.2(29)	72.9(52)	...	90.4(52)	83.8(8)	...	76.7(35)	63.5(14)
XII	58.5(97)	65.0(52)	67.9(20)	73.1(50)	...	91.2(29)	86.5(15)	...	76.5(26)	63.9(27)
XIII	59.0(53)	64.5(19)	71.4(28)	75.3(30)	...	91.9(20)	...	...	82.5(19)	65.8(37)
XIV	62.2(25)	67.5(12)	75.9(11)	77.1(22)	...	95.8(10)	...	...	...	67.5(20)
XV	63.5(10)	...	...	...	...	...	...	...	...	...
XVI	...	...	...	81.4(21)	...	...	...	...	...	...

In the southwestern part of the area (Fig. 3c), St. Pierre Bank fish are somewhat smaller at the younger age-groups (up to VI) than fish from the southwest coast of Newfoundland and fish from both sections of the Grand Bank. However, the differences are not great. At ages beyond the VII-group the St. Pierre Bank and southwest Newfoundland fish are intermediate in size between the southwestern and northeastern Grand Bank fish.

In the western area (Fig. 3D), off the west coast of Newfoundland, cod are somewhat larger than those of comparable age-groups from eastern Newfoundland but slightly smaller than those from southwestern Newfoundland.

The growth curve for Strait of Belle Isle cod exhibits an interesting peculiarity (Fig. 3D). For younger age-groups up to VIII the curve is almost coincident with the growth curve of fish from the west coast of Newfoundland after which it diverges to join the growth curve of fish from the northern section of the east coast.

Growth in Weight

Not as many observations were made on weights of fish as on the lengths, but information gathered indicates a trend of differences between average weights of corresponding age-groups of cod from different localities similar to that found for average lengths. Table III gives the average weights of the age-groups in the various geographical subdivisions of the area and Fig. 4 expresses the information graphically and with the curves grouped for comparison.

There is considerable variation in the individual weights of fish of the same age-group in any locality. This variation is much more pronounced in the older fish than in the younger, and more in cod exhibiting rapid growth than in those of slow growth.

Differences between regions are quite pronounced in the average weights of the older age-groups, but are much smaller in the younger age-groups. As the curves diverge at the older age-groups some irregularities occur in many of them, due in some degree to lack of numbers in some age-groups and the large variation in individual weights in the particular age-groups concerned.

Growth of the Otolith

Otoliths are found in the sacculus. An otolith is roughly spindle-like in outline, but somewhat curved with one side convex, the other concave. Hickling (1931) investigated the microscopic structure of the otolith of the hake, a gadid closely resembling the cod. He found the otoliths to be comprised of two constituents, an inorganic, crystalline constituent, and an organic, fibrous one. Growth of the otolith occurred by the addition of layers of these constituents over its entire outer surface. The organic part of the otolith was in the form of a series of concentric shells of lamellae bound together by radial fibres and supported by the inorganic, crystalline part. The lamellae were grouped in such a way that alternate zones of thick and thin lamellae occurred, with the

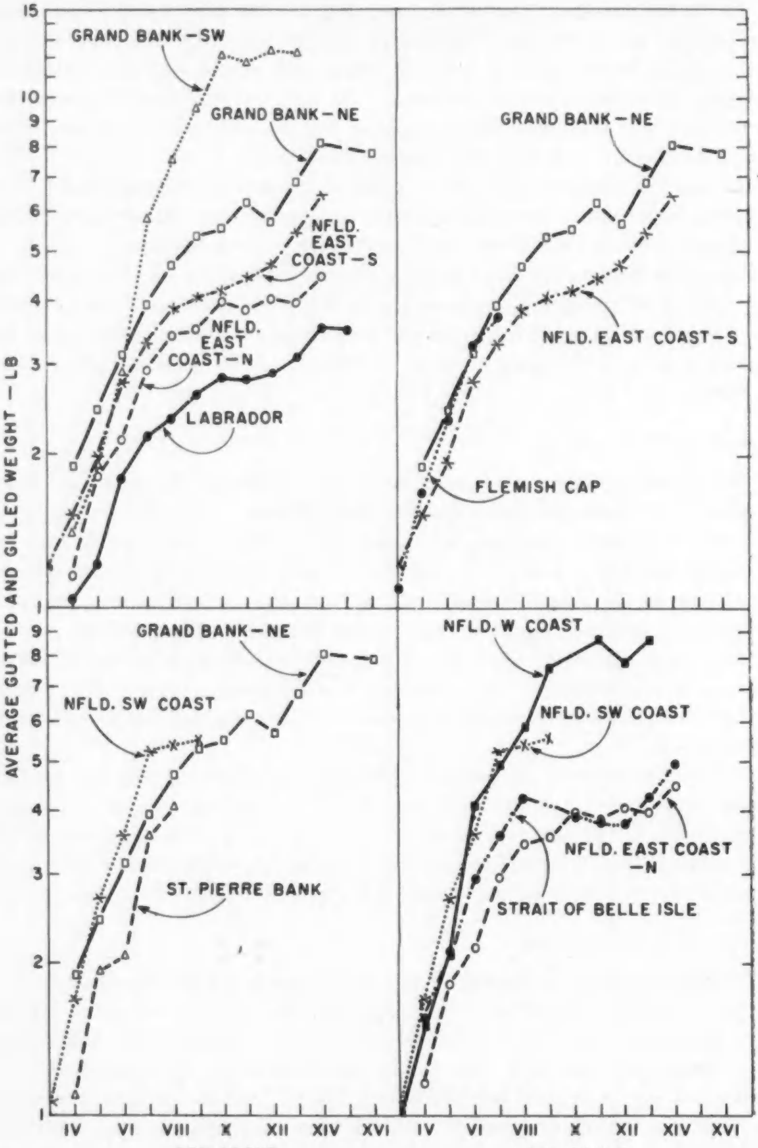

FIG. 4. Semilogarithmic plot of average weights (gutted and gilled, in pounds) of the different age-groups of cod from various localities, Labrador and Newfoundland, 1947–1950.

TABLE III. Average weights (gutted and gilled, in pounds) of different age-groups from various localities off Labrador and Newfoundland, 1947–1950. (Numbers of fish in parentheses.)

Age group	Labrador	E coast, N portion	E coast, S portion	Grand Bank, NE portion	Flemish Cap	Grand Bank, SW portion	St. Pierre Bank	SW coast	W coast	Strait of Belle Isle
	lb	*lb*	*lb*	*lb*	*lb*	*lb*	*lb*	*lb*	*lb*	*lb*
III	...	0.76(8)	1.20(5)	...	1.08(4)	...	...	1.06(40)	1.01(10)	...
IV	1.03(9)	1.16(34)	1.52(60)	1.90(3)	1.69(47)	1.40(4)	1.10(14)	1.69(35)	1.51(55)	1.57(3)
V	1.22(13)	1.81(38)	1.92(104)	2.43(9)	2.35(15)	1.92(5)	1.95(43)	2.68(109)	2.07(49)	2.09(31)
VI	1.80(122)	2.14(31)	2.76(67)	3.16(18)	3.28(31)	2.91(7)	2.07(13)	3.58(64)	4.13(25)	2.93(12)
VII	2.18(33)	2.96(60)	3.30(65)	3.93(40)	3.76(17)	5.79(27)	3.58(5)	5.24(27)	4.93(29)	3.57(20)
VIII	2.34(84)	3.44(34)	3.82(54)	4.70(40)	...	7.51(54)	4.06(7)	5.37(26)	5.87(19)	4.25(18)
IX	2.61(55)	3.52(60)	4.06(72)	5.33(59)	...	9.50(34)	...	5.52(14)	7.68(12)	4.10(33)
X	2.83(55)	3.99(40)	4.18(49)	5.52(46)	...	12.10(30)	...	...	...	3.96(17)
XI	2.80(85)	3.86(34)	4.44(29)	6.26(33)	...	11.67(35)	...	...	8.71(12)	3.78(13)
XII	2.89(93)	4.07(52)	4.70(20)	5.68(36)	...	12.48(22)	...	...	7.84(11)	3.76(26)
XIII	3.13(52)	3.99(19)	5.44(28)	6.84(20)	...	12.26(16)	...	...	8.71(10)	4.29(32)
XIV	3.58(25)	4.48(12)	6.45(11)	8.16(11)	...	...	...	...	...	4.95(15)
XV	3.52(10)	...	...	...	...	...	...	...	...	...
XVI	...	...	...	7.86(12)	...	...	...	...	...	...

regions of thick lamellae appearing relatively opaque, the regions of thin lamellae translucent.

Cod otoliths show similar zonation. E. Dannevig (1956) investigated the chemical composition of the zones in cod otoliths. She stated that two of these zones were formed each year, an opaque zone and a transparent zone. She found that the inorganic constituent of the otolith, consisting of calcium compounds, was present in both types of zones but that the organic constituent, consisting of a protein, conchiolin, was present only in the opaque zone.

In this paper it is assumed that the opaque zones are associated with periods of greatest growth of the otolith, for they are much thicker than the translucent ones; and that the formation of one opaque and one translucent zone marks one year in the life of the fish. Also, it is assumed that the period of greatest growth in the otolith is associated with the period of greatest growth in length of the fish.

Table IV shows the condition of the outside of the otolith in fish from various regions at different months of the year. Although only a small amount of data is available, it is enough to show differences between some regions in the time of formation of the opaque layer, that is, in the time of greatest growth.

TABLE IV. Condition of zone at the edge of the otolith during different months in various regions. For each region the top figures represent the number of cod having otoliths with a translucent (narrow) zone at the edge, the bottom figures represent the number with an opaque (wide) zone at the edge. Only otoliths older than age-group III have been used.

Region	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.
Labrador	...	...	...	...	331	332	...	...	...
					0	0			
Nfld. east coast N	...	...	...	104	108	134	53	...	...
				1	1	1	20		
Nfld. east coast S	...	...	...	...	114	215	29	72	50
					0	10	15	27	70
Grand Bank NE	...	...	...	232	226	...	...	...	...
				0	1				
Flemish Cap	...	...	...	...	237	...	...	...	...
					1				
Grand Bank SW	...	224	199	...	100	...	...	...	...
		0	0		12				
St. Pierre Bank	94	108	...	73	48	...	...	...	...
	0	0		1	3				
Nfld. SW coast	...	...	...	240	...	...	...	...	...
				61					
Nfld. W coast	...	...	...	...	107	149	...	...	4
					66	133			101
Strait of Belle Isle	...	...	...	...	235	...	...	...	...
					31				

Contrary to popular belief the deposition of the opaque zone in the otolith does not occur chiefly during summer when the air temperature over the sea is warmest, but somewhat later, when higher temperatures, 2 to 3°C, are distributed to greater depths. The time of deposition does not generally coincide with the time of greatest feeding. The heaviest feeding apparently occurs after spawning, on capelin or herring in many inshore areas and launce and capelin on the banks. The fast during spawning and the spawning itself have somewhat starved the fish so that the heavy feeding serves not for growth but for restoration of liver fat and flesh proteins which have been much reduced. Following the build-up of these organs fast growth begins and is registered as the opaque zone at the edge of the otolith.

Our examination showed great variation in the time of beginning of opaque zones at the otolith edge, even in the same area, and even in November, the latest month of our collecting, the opaque zone was not visible at the otolith edge in some fish. With greater experience it is likely that the beginning of the opaque zone at the otolith edge might be recognized earlier than has been shown for each region. However, since all observations were made by the same person (the author), the relative times of appearance of the zones for different regions are reasonable.

Labrador fish taken in July and August were all found to have a translucent zone at the edge of the otoliths. It is apparent that the beginning of the opaque zone on the otolith edge occurs later in the year, probably in September, for Labrador fish than for fish from any other locality. On the east coast of Newfoundland, the northeast portion of the Grand Bank and Flemish Cap the beginning of the opaque zone occurs earlier in the year, probably in late June for east coast fish and early in July for fish from the northeastern Grand Bank area. On the southwest portion of the Grand Bank the opaque edge begins probably in June, presumably somewhat before the time of appearance of the opaque edge on otoliths of fish to the north. Indications are that for fish on St. Pierre Bank the first appearance of the opaque edge occurs at about the same time as for the southwest Grand Bank cod. The southwest coast fish would have the beginning of the opaque edge earlier than for the bank areas, probably in May. That so many of the west coast fish have the opaque layer at the edge of the otolith in July is an indication that the first appearance of the opaque edge must occur several weeks earlier. Considerably less of the fish from the Strait of Belle Isle region have opaque growth at the edge of the otolith than west coast fish taken at the same time, and on this basis are closer in their resemblance to east coast than to west coast fish.

Comparison with Data of Other Workers

For Labrador cod comparable growth data of several investigators in the area are shown with our data for 1948 (Table V). Differences exhibited between the sets of data are probably due to a combination of effects.

Differences in locations from which the samples were taken and in the sampling gears undoubtedly contributed to the differences shown. Though

TABLE V. Comparison of average size of various age-groups of cod as found by different investigators in the area. Ruivo's figures were taken from Poulsen (1957), and Rojo's figures from Figueras (1957).

Investigator	Years	Average size of each age-group											
		II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII
		cm	*cm*	*cm*	*cm*	*cm*	*cm*	*cm*	*cm*	*cm*	*cm*	*cm*	*cm*
A. LABRADOR													
Thompson	1931–35	26.7	36.5	43.1	49.5	57.0	61.6	65.2	70.6	79.2	89.5	96.4	105.5
Ancellin	1952	...	38.5	46.2	48.7	52.4	56.0	58.3	61.0	62.9	65.4	...	...
Ruivo	1955	...	33	39	44	47	51	53	55	55	57	...	...
Fleming	1948	...	...	41.1	43.6	48.8	51.8	54.2	56.2	58.4	57.8	58.5	...
B. GRAND BANK													
Thompson	1931–35	27.0	35.0	44.4	53.5	60.5	68.7	76.4	84.1	93.8	99.6	106.0	109.9
Ancellin	1951	22.3	30.6	42.2	53.1	58.8	70.4	76.0	79.0	85.1	...	...	...
Rojo[a]	1953, 1956	...	...	...	52.5	57.5	64	70	...	...	...	...	...
Figueras[b]	1955	22	37.3	46.3	53.1	60.6	67.0	78.3	...	...	...	...	...
Fleming[b]	1947–50	...	...	48.0	52.7	57.8	62.2	66.2	69.5	71.0	72.9	73.1	75.3
Fleming[a]	1947–50	...	44.0	49.0	51.6	59.7	69.8	76.9	83.5	87.6	90.4	91.2	...

[a]From southwest Grand Bank.
[b]From northeast Grand Bank.

Thompson (1943) did not state how his Labrador samples were collected, we have ascertained that they were collected from the gears of inshore fishermen, probably from cod traps. Ancellin's (1954) samples were taken entirely from offshore catches by a research otter-trawl. Ruivo (1957) used samples from the gears of commercial otter-trawlers fishing offshore. Our 1948 samples were from various gears of inshore fishermen in relatively shallow water (Table I).

Examination of individual samples of cod from Labrador reveals a slight decrease in growth rate with increase in latitude. Most of Thompson's samples were from the southern portion of Labrador. Both Ancellin's and Ruivo's samples came from the vicinity of Hamilton Inlet Bank (Fig. 1). Of 6 samples collected in our 1948 study, 4 were from localities in the northern part of Labrador.

For the Grand Bank cod, comparable data of Thompson (1943), Ancellin (1954), Rojo (1955) and Figueras (1957) are shown with our 1947–1950 data (Table V). On the Grand Bank there is a wide difference in the rate of growth between cod from the northeast and southwest portions. For this reason we have distinguished between the two regions and have kept samples from the two separate. Thompson and Ancellin in each case have combined samples from the northeast and southwest sections of the Grand Bank, Figueras' samples were from the northeast section, Rojo's from the southwest. Thus, in a comparison of the Grand Bank cod average growth rates found by these authors, we have brought together samples of fish with widely different growth rates.

Hansen (1949) has demonstrated that different year-classes in the same area can have different rates of growth, and, since not all the same year-classes were involved in each study, this may have contributed to the differences in the results of the various investigators.

Finally, errors in age estimation by the different investigators would cause differences in results. Thompson used scales for age determination; all other investigators used otoliths. It has been demonstrated by many investigators (A. Dannevig, 1933; Rollefsen, 1933; Hansen, 1949) that scales are inferior to otoliths for age determination in cod, except in very young fish. The scale method has a tendency in older fish to give lower age values and, consequently, a more rapid growth rate than the otolith method. The otoliths of cod in the Grand Bank area especially, however, are often difficult to interpret because of various secondary zones. This results in differences in reading by different persons and consequent differences in growth rates calculated from these readings.

SEXUAL MATURITY

Size at Sexual Maturity

Figure 5 shows the percentages of immature and mature cod found at various sizes in the combined sample from each region. It is readily seen that more fish are sexually mature at the smaller sizes in Labrador than in any other region. In each locality all fish were immature at 40 cm in length but in Labrador some fish were mature in the 42 to 43 cm group, and all were mature at the 52 to 53 cm group.

Along the east coast and in the northeast Grand Bank region, considerable numbers of sexually mature fish were found below 60 cm in length and practically all fish were mature at 65 cm in the east coast region and 70 cm in the northeast Grand Bank and Flemish Cap regions.

In the southwest Grand Bank region, however, sexually mature fish were generally larger, there being relatively few matures below 60 cm in length and some fish still immature up to 90 cm in length.

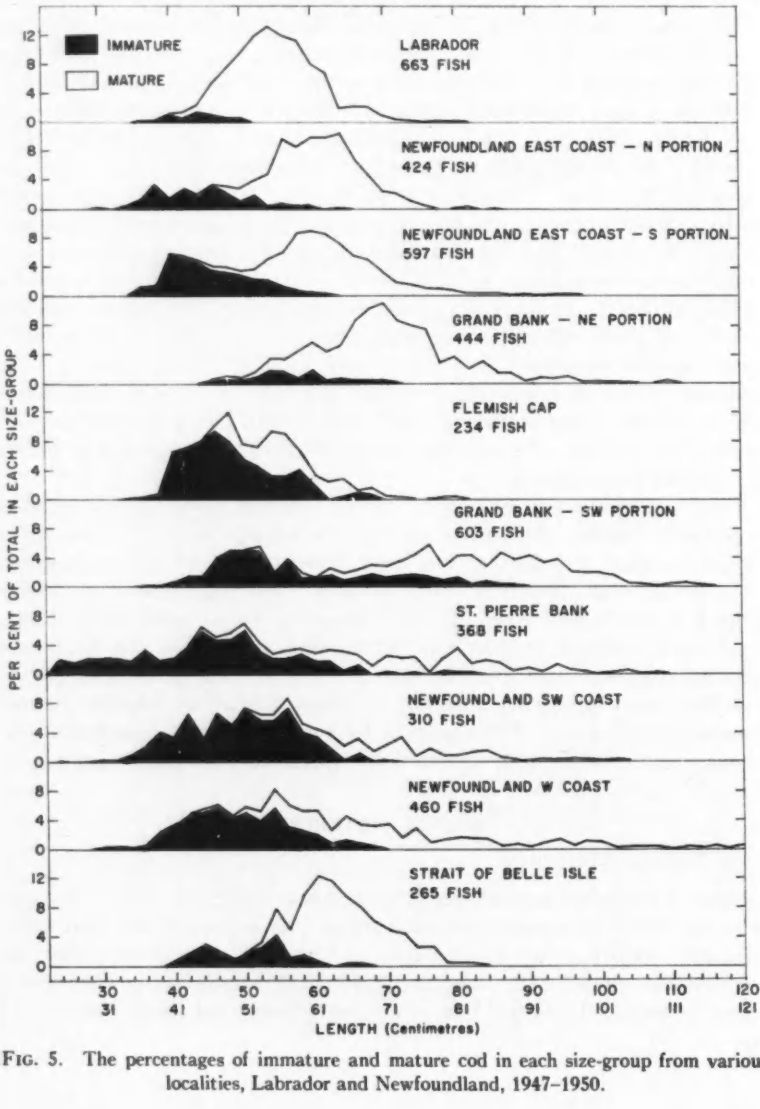

FIG. 5. The percentages of immature and mature cod in each size-group from various localities, Labrador and Newfoundland, 1947–1950.

To the west, cod from St. Pierre Bank and the southwest and west coasts of Newfoundland mature first at somewhat smaller sizes than cod of the southwest Grand Bank. Sexually mature fish were found at 50 cm in these three regions, but all fish in the coastal regions were mature at about 70 cm, 10 cm smaller than on St. Pierre Bank.

In the Strait of Belle Isle samples, the incidence of sexually mature fish was much lower at sizes below 60 cm than in the west coast samples, though all fish were not mature until about 70 cm in both regions.

Age at Sexual Maturity

It is obvious that the absolute yearly increase in length of cod from each locality is not constant throughout life (Fig. 3). The most rapid increase is in the earlier age-groups, followed by a period of slower increase.

Cod in samples from the different localities were all found to be immature in age-group III and all sexually mature in age-group XI. From the IV-group to the X-group increasing proportions of the fish were found to be mature. Although the numbers of fish in the samples are not great enough for fine analyses, it is indicated that the onset of sexual maturity does not occur in every place at the same fish age or size. In some localities fish were found to be mature in the IV-group, and in all localities some mature fish were found in age-group V, but the incidence varied; similar conditions were found for succeeding age-groups. As a result the first age at which all fish were found mature was variable.

Figure 6 shows the composition by age-groups of combinations of samples from the various subdivisions of the area. Labrador fish mature rapidly. Though only 8% of the fish in the Labrador sample were mature in the V-group, all were mature in the IX-group. Designating fish in age-group I as 1 year old, those in age-group II as 2 years old, etc., the age at which 50% of the fish are sexually mature in each region has been calculated using the "LD_{50}" procedure (Bliss, 1935a, b, 1952; Mather, 1946), as applied by Stanley and Slatis (1955) to *Tribolium* experiments. The method was originally used to assess the effects of different doses of poisons. In Stanley and Slatis' application the animals are "dosed" with time and it is required to find the time at which 50% have transformed to the next stage.

Table VIa is a worked-out example for the cod of the west coast of Newfoundland, to illustrate the method. The first step to arrive at a provisional line is to convert the values for the percentages of fish sexually mature at each age to empirical probits (Table IX, Fisher and Yates, 1948). The probits for 0 and 100% cannot be determined at this stage. The empirical probit values are now plotted as ordinates against age in years and a straight line is fitted to the plot by inspection. New, expected probits (Y) are then read off the line for each age and are used in the computation of a new line. For this line weighting coefficients can be found for each probit value (Table XI, Fisher and Yates, 1948) and the relative weight (w) assigned to each by multiplying the weighting coefficient at each age by the number of fish examined at the same age. When the expected probit values are less than 5.0, the working probit (y) equals the minimum

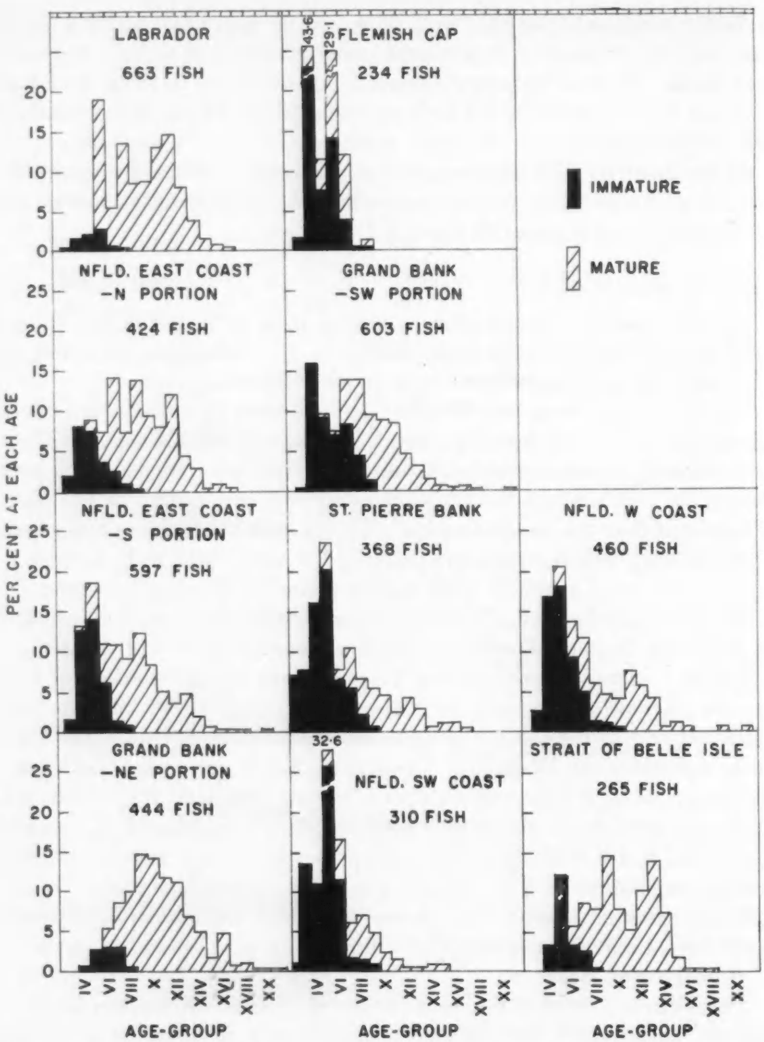

FIG. 6. The percentages of immature and mature cod in each age-group from various localities, Labrador and Newfoundland, 1947–1950.

working probit plus the correction factor. When expected probit values are 5.0 and greater, the working probit equals the maximum working probit minus the correction factor. The correction factor equals the proportion mature (P) × Range for probits where P is 0.5 or less, and the proportion immature (Q) × Range for probits where P is greater than 0.5 (Table XI, Fisher and Yates, 1948).

TABLE VIa. Computations for fitting line to data on the development of sexual maturity with age in the sample from the west coast of Newfoundland.

	Data for provisional line					Computation of weighted line					
Age	No. of fish	No. of matures	Percent mature	Percent immature	Empirical probit	Expected probit	Weighting coefficient	Weight	Working probit	Intermediate products	
X	N	E	P	Q		Y		w	y	wx	wy
3	8	0	0.0	100.0	...	2.3	0.03143	0.251	1.97	0.753	0.494
4	78	2	2.6	97.4	3.06	3.2	0.17994	14.035	3.07	56.140	43.087
5	111	28	25.2	74.8	4.33	4.1	0.47144	52.330	4.36	261.650	228.159
6	65	29	44.6	55.4	4.86	5.0	0.63662	41.380	5.14	248.280	212.693
7	64	58	90.6	9.4	6.32	5.9	0.47144	30.172	6.24	211.204	188.273
8	53	49	92.5	7.5	6.44	6.8	0.17994	9.537	6.31	76.296	60.178
9	72	72	100.0	0.0	...	7.7	0.03143	2.263	8.03	20.367	18.172
10	49	49	...	...	...	...	...	...	...	...	...

$\Sigma w = 149.968$

$\Sigma wx = 874.690$

$\bar{x} = \Sigma wx/\Sigma w = 5.833$

$\Sigma wy = 751.056$

$\bar{y} = \Sigma wy/\Sigma w = 5.008$

$\Sigma wx^2 = 5296.848$

$\Sigma wxy = 4555.842$

$\Sigma wy^2 = 3921.733$

$A = \Sigma wx^2 - \bar{x}\Sigma wx = 194.781$

$B = \Sigma wxy - \bar{x}\Sigma wy = 174.932$

$C = \Sigma wy^2 - \bar{y}\Sigma wy = 160.445$

$\text{Slope} = m = B/A = 0.897$

$$\text{Age at 50\% maturity} = M_{50} = \bar{x} + \frac{(5.0 - \bar{y})}{m} = 5.824$$

$$\text{Variance} = V = \frac{1}{m^2}\left[\frac{1}{\Sigma w} + \frac{(M_{50} - \bar{x})^2}{A}\right] = 0.007458$$

$$\text{Standard error} = \sqrt{V} = 0.086$$

χ^2 for goodness of fit of weighted line:

$$\chi^2 = C - mB = 3.531$$

$$\text{d.f.} = n = 5 - 2 = 3, \quad \chi^2 \text{ for } P_{05} = 7.815$$

$$\text{Standard error of } m = \sqrt{\frac{\chi^2}{nA}} = 0.041$$

Equation of weighted line:

$$Y_e = \bar{y} + m(x - \bar{x}) = 0.897x - 0.224$$

TABLE VIb. The expected number of mature fish at each age from the computed line ($Y_e = 0.897x - 0.224$), and the grouping used for assigning degrees of freedom for the chi-square test.

	Original data		Data from computed line			
Age X	No of fish N	No. of matures E	Probits Y_e	Percent mature P_e	No. of matures E_e	Degrees of freedom
3	8	0	2.47	0.6	0.05	1
4	78	2	3.36	5.1	4.0	
5	111	28	4.26	23.0	25.5	1
6	65	29	5.16	56.4	36.7	1
7	64	58	6.06	85.5	54.7	1
8	53	49	6.95	97.4	51.6	
9	72	72	7.85	99.8	71.9	1
10	49	49	8.75	100.0	49.0	

The chi-square test has been used to ascertain how well the experimental observations fit the computed line. When the scatter of the points about the fitted line is no wider than would be expected by chance at a probability of 0.05, i.e. when the chi-square is no larger than the chi-square for a probability of 0.05, the data are considered to fit the computed line. The computation of chi-square is relatively straightforward but its significance depends upon the number of degrees of freedom allowed. Bliss (1935a) indicates that, of the total allowed, one degree of freedom is lost in establishing the position of the computed line and one in establishing the slope of this line. Small expected values have been combined at either end of the distribution (Table VIb).

Table VII shows some of the data for the computed curves from the different areas. Only in the Labrador sample are the observed data not consistent with the fitted line at the P = 0.05 level, but in that instance the chi-square value lies below the P = 0.02 level. The deviation, if it is real, may be due to the very short range of ages over which the development of maturity occurred and the relatively small number of immature fish in this sample.

The age at which 50% of the fish in the Labrador sample were sexually mature (M_{50}) is about 5.4 years (Fig. 7, Table VII). This is statistically different at the 5% level from the comparable age in samples from each of the other regions tested.

Though some variation exists in the immature–mature composition of comparable age-groups in samples from Newfoundland's east coast, the northeast part of the Grand Bank, and Flemish Cap, these differences are not great. The east coast fish were somewhat later in attaining sexual maturity than the Labrador fish and the age at which 50% were mature was from 5.8 to 6.1 years. On Flemish Cap 50% were found mature at 6.0 years and on the northeast part of the Grand Bank at 6.3 years. On the basis of the 50% maturity point, there

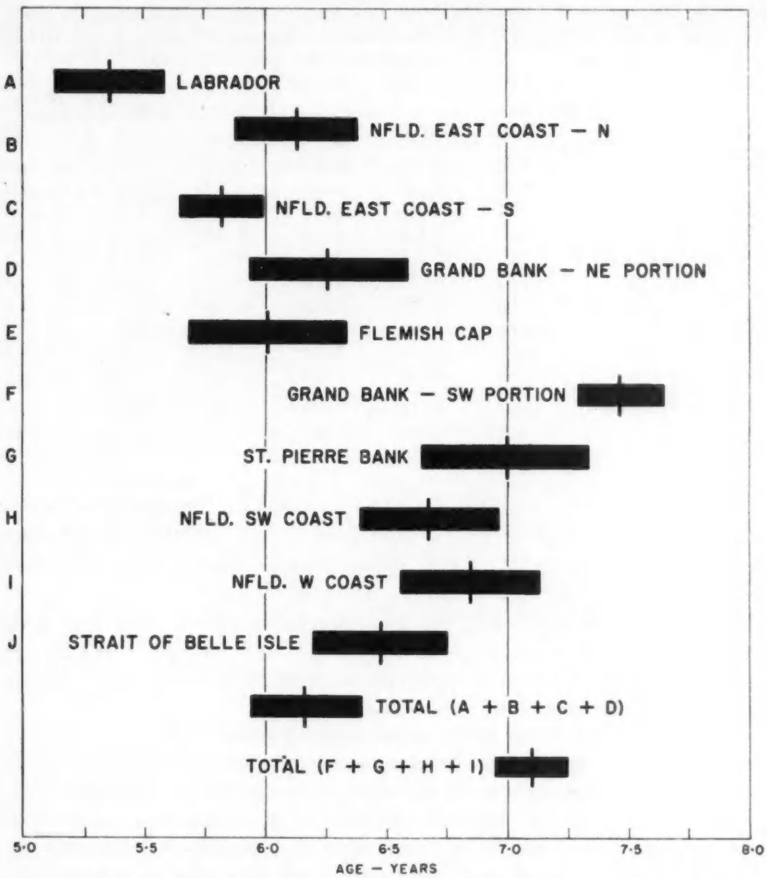

FIG. 7. Age at which 50% of the cod were mature in samples from various localities, Labrador and Newfoundland, 1947–1950. The vertical bar represents the mean, the rectangle the limits of twice the standard error of the mean.

is no statistical significance at the 5% level in the differences in the times of maturity of cod from the east coast of Newfoundland, northeast Grand Bank and Flemish Cap.

To the south, however, in the southwest Grand Bank region, fish are generally later in reaching sexual maturity; the age at which 50% were mature was 7.5 years. Few fish were mature in age-group V and all fish not mature until group X. To the north, all fish except about 1% from the east coast of Newfoundland were mature in the IX-group.

On St. Pierre Bank group X was the youngest age-group in which all fish were sexually mature. The 50% maturity point occurred at 7.0 years.

TABLE VII. The age at 50% maturity (M_{50}), the slope (m), the standard errors (SE) of these, and the chi-square for the computed lines representing the incidence of sexually mature individuals at successive ages in samples from the different regions.

Area	M_{50}	SE(M_{50})	m	SE(m)	"Fit" of line X^2	d.f.	$X^2(P_{05})$
A. Labrador	5.36	0.111	1.375	0.360	7.682	2	5.991
B. Nfld. east coast N	6.13	0.125	0.831	0.121	6.311	3	7.815
C. Nfld. east coast S	5.82	0.086	0.897	0.041	3.531	3	7.815
D. Grand Bank NE	6.26	0.163	0.948	0.168	3.393	2	5.991
E. Flemish Cap	6.01	0.163	0.701	0.109	4.276	3	7.815
F. Grand Bank SW	7.47	0.090	0.864	0.086	5.066	3	7.815
G. St. Pierre Bank	7.00	0.168	0.640	0.125	4.858	3	7.815
H. Nfld. SW coast	6.68	0.145	0.870	0.121	4.285	3	7.815
I. Nfld. W coast	6.85	0.141	0.620	0.055	4.293	4	9.488
J. St. of Belle Isle	6.48	0.138	1.108	0.131	1.109	1	3.841
Total (A to D)	6.17	0.114	0.949	0.092	12.908	4	9.488
Total (F to I)	7.10	0.072	0.669	0.042	9.548	5	11.070

In samples from the southwest and west coasts of Newfoundland the ages of 50% maturity (6.7 and 6.9 years respectively) were not significantly different at the 5% level from the St. Pierre Bank samples, though they were distinct from the southwest Grand Bank fish on this basis.

In the Strait of Belle Isle the fish matured rapidly. The first sexually mature fish appeared in the V-group and all fish were mature in the IX-group. These fish were intermediate between the west coast and east coast fish as far as the 50% maturity point (6.5 years) was concerned.

The ranges of age over which sexual maturity takes place in cod from the various areas are represented by the slopes of the computed lines for these areas. These differ from area to area (Table VII). Comparison of samples from the cold eastern area (A to D) with the warmer south and western areas (F to I) indicates a much longer time over which development of sexual maturity occurs in the warmer area than in the colder one. The difference between the slopes of the two lines is 0.280 with a standard error of 0.101. Using ∞ degrees of freedom (t = 1.96 at P = 0.05) we find this difference is significant (t = 2.77).

SEX RATIO

As is well known for many species of fish, male cod generally mature at a slightly younger age and smaller size than the females. Thus, if there were a greater preponderance of one sex over the other and this were variable from region to region, the relative over-all picture of maturity in the separate samples probably would be significantly affected. If males largely outnumbered females, the general effect in a sample would be to show the beginnings of maturity at an earlier age and smaller size than if females made up the majority. A determination of the sex ratio by age-groups for the sample from each region showed that the effects of sex ratio on the relative times of maturity is not great. There

is no trend toward a progressively greater preponderance of one sex with increase in age in any of the samples.

In Table VIII the average sex ratio for each region as based on the combination of all the age-groups is shown. In 8 of the 10 regions females outnumbered the males in the samples. Only in the southwest Grand Bank and St. Pierre Bank samples were there more males than females. Despite this, maturity in these two regions is relatively late.

TABLE VIII. Average sex ratio of cod in each region. Ratio is expressed as number of females per 100 males.

Region	Number of males	Number of females	Sex ratio 100(female ÷ male)	Percentage males
Labrador	331	333	101	49.8
Nfld. east coast N	164	265	162	37.2
Nfld. east coast S	271	337	124	44.6
Grand Bank NE	189	270	143	41.1
Flemish Cap	110	125	114	46.7
Grand Bank SW	333	280	84	54.3
St. Pierre Bank	196	175	89	52.8
Nfld. SW coast	136	233	171	36.8
Nfld. W coast	215	247	115	46.5
St. of Belle Isle	101	165	163	37.9
Total	2,046	2,430	114	45.7

DISCUSSION AND CONCLUSIONS

Results of other investigators working in the Newfoundland and Labrador regions have indicated that cod found in the area do not consist of one large homogeneous population, but rather that the population is divided into relatively distinct groups. These divisions of population continue to exist because of the small degree of inter-migration between cod from the different groups.

INFORMATION FROM TAGGING. Thompson (1943) carried out extensive tagging of cod at various points in the Newfoundland area and found that the largest proportion of the tagged fish were captured relatively near the points of tagging. Both Thompson's tagging and the experiments described by Templeman (1951, 1953) have demonstrated similar general patterns of cod migration in the Newfoundland and Labrador regions.

There were considerable individual movements of cod along the east coast of Newfoundland and some movement southward from Labrador to the east coast of Newfoundland. Also, some exchange was evident between the southern part of the east coast and the northern area of the Grand Bank. No recaptures of fish tagged in the east coast region were recorded from the southern part of the Grand Bank, or vice versa. No migration was demonstrated between the northern and southern portions of the Grand Bank, but there was some exchange between the western portion of the Grand Bank and St. Pierre Bank.

From tagging on St. Pierre Bank recaptures indicated a fairly widespread movement of cod to other banks and to various points along the south coast of Newfoundland, with a high proportion of the recaptures indicating comparatively long migrations.

Tagging experiments on the west coast of Newfoundland indicated a southward movement of cod out of the Gulf of St. Lawrence on the Newfoundland side to the southwest coast of Newfoundland in the early winter and a return migration to the Gulf in the spring, northward along the west coast of Newfoundland as far as the Strait of Belle Isle.

Thompson (1943) found it noteworthy that no cod tagged in the Gulf of St. Lawrence was captured off the Labrador coast outside the Gulf to the north. Some recaptures of cod tagged outside the Gulf, off Labrador, and on the east coast of Newfoundland were made in the inner part of the Strait of Belle Isle, in the northern part of the Gulf, but none were reported from any great distance inside the Gulf. Similarly, in the south, no recapture was recorded in the Gulf of St. Lawrence of cod tagged on the eastern part of the south coast or on St. Pierre Bank and the Grand Bank.

INFORMATION FROM SCALE STRUCTURE. Thompson (1943) used the number of circuli in the first year of the cod scale as a criterion for distinguishing between groups of cod in the Newfoundland area. On the basis of average numbers of circuli he distinguished between three types of cod. The arctic type, influenced by the colder portion of the Labrador Current (average number of circuli: 7.8–9.7), included cod from Labrador, the east coast of Newfoundland and the northeast portion of the Grand Bank. In this group the average number of circuli was found to increase somewhat from north to south in the area of distribution. The bank type, influenced by warmer Atlantic water (average number of circuli: 10.6–12.1), included cod from the south and southwest portions of the Grand Bank and from St. Pierre Bank. The Gulf of St. Lawrence type, influenced by intermediate temperature conditions (average number of circuli: 10.0), consisted of cod from the Gulf of St. Lawrence.

INFORMATION FROM NUMBER OF VERTEBRAE. Schmidt (quoted by Thompson, 1943) had used numbers of vertebrae to distinguish between classes of cod in the North Atlantic Ocean and his results were confirmed for the Newfoundland area by Thompson. On the basis of vertebral averages, Thompson distinguished between two types of cod in the Newfoundland area: one influenced by the warm Atlantic water, inhabiting the more southern parts of the area and having low average vertebral numbers; and another influenced by cold arctic water, in the Labrador and Newfoundland east coast regions, mainly with a high average vertebral number. Templeman (1953) reports that vertebral averages of cod from the Labrador region, the Newfoundland east coast and the northern edge of the Grand Bank were not inconsistent with the existence of a single population over that extensive area. The averages of vertebral numbers (not including the hypural) are over 54 along the east coast of Newfoundland to the northern edge of the Grand Bank and along the coast of Labrador. On the other hand the

vertebral averages showed that cod taken in regions from Labrador to the northern part of the Grand Bank were different from those occupying the body of the bank and, in particular, cod from the southern part of the bank, where the average was usually below 53. For St. Pierre Bank, cod vertebral averages were generally intermediate between the high values of the eastern region and the low values both to the south and west. Vertebral averages of cod along the southern half of the west coast of Newfoundland (usually below 53) were consistent with the existence of a fairly distinct body of cod in this region. Gradually increasing vertebral averages in the northern part of the west coast proceeding northward to the Strait of Belle Isle were consistent with an apparent seasonal migration of fish from the east coast into the northern part of the Gulf in the Strait of Belle Isle area.

INFORMATION FROM INCIDENCE OF PARASITISM. A study of the incidence of nematode parasites in the fillets of cod in Newfoundland and neighbouring areas (Templeman, Squires and Fleming, 1957) revealed a variation in the degree of infection. For the areas concerned in the present study the rate of infection of cod with nematodes was highest on the west coast of Newfoundland, 21–49%. It was fairly high on the southwest coast of Newfoundland, 20–29%; and on the northern part of St. Pierre Bank, 14–29%. Infection was low on the southern part of St. Pierre Bank, on the Grand Bank, Flemish Cap, the east coast of Newfoundland and off Labrador, 0–7%. The nematodes involved in the infection were *Porrocaecum* and *Anisakis*. In cod from the Newfoundland south coast, west coast and St. Pierre Bank between 92 and 98% of the nematodes were *Porrocaecum*; in the Newfoundland east coast and Labrador inshore areas between 84 and 100% were *Porrocaecum*. In the distant offshore areas such as Grand Bank and Flemish Cap much higher percentages of *Anisakis* were included. Thus, if only the *Porrocaecum* infection is considered, the differences between areas will be even more pronounced, revealing high infections on the west and southwest coasts, low infections on the east coast and Labrador and very low infections in areas of the Grand Bank farthest offshore.

The degree of infection of cod by *Porrocaecum* was attributed mainly to the relative abundance of the nematode's primary hosts, the harbour seal, *Phoca vitulina*, and the grey seal, *Halichoerus grypus*, and associated intermediate hosts in the various regions.

INFLUENCE OF OCEANOGRAPHIC CONDITIONS. Some knowledge of the hydrography (physical oceanography) in the Newfoundland area will assist in explaining differences in growth and sexual maturity found in cod from various regions of the area. Many investigators, including Bjerkan (1919), Smith, Soule and Mosby (1937), Thompson (1943), Bailey and Hachey (1951) and Bailey, Templeman and Hunt (1954) have contributed to the knowledge of hydrographic conditions in the area.

The eastern region from Labrador southward along the east coast of Newfoundland to the northern part of the Grand Bank is under the influence of the landward portion of the Labrador Current which flows southward along the

Labrador and Newfoundland east coasts. At the Strait of Belle Isle a portion of the water passes westward through the Strait on the north side. The main portion of the current, however, continues southward along the east coast of Newfoundland until it strikes the northern face of the Grand Bank. Here it is divided, with the main branch continuing southward along the eastern edge of the bank, and a smaller branch passing through the channel to the west between the bank and the coast.

The landward portion of the Labrador Current is present in the eastern region in spring and summer as a cold middle layer of water with temperatures from 0°C to less than −1°C, which enters all the bays, reaches to the bottom in the inshore areas and extends seaward for many miles. Near shore in water shallower than this cold middle layer and seaward in water deeper than the cold layer, temperatures are suitable for cod of the area. Where the cold waters are in contact with the northern face of the Grand Bank, they form an effective temperature barrier which prevents cod in the deeper northern areas from moving up over the face of the bank to the shallower waters on the top of the bank.

In the southwest of the Grand Bank and westward in the St. Pierre Bank area the confluence of the Labrador Current and the Gulf Stream occurs (Hachey *et al.*, 1954). Here, large scale mixing provides a type of "slope water" which reduces the dominant cold influence of the northern water and this southern region is much warmer than areas to the north.

The Newfoundland west coast region is protected to a great degree by land masses and is not subjected to the direct colder influence of the Labrador Current from the north or the warmer oceanic waters from the south, and generally, intermediate temperature conditions are found to exist. In the Strait of Belle Isle area, however, cold Labrador Current water flows into the area on the Labrador side while warmer water from the west coast of Newfoundland flows out on the Newfoundland side of the Strait.

COD STOCKS OF NEWFOUNDLAND WATERS. The age, growth and sexual maturity relationships of cod from various parts of the area, when analysed in the light of tagging experiments, meristic studies, parasite studies and hydrographic information, suggest the existence of at least four relatively distinct subdivisions in the cod population of the area, between which there is apparently only limited intermingling. These are the Labrador, the Newfoundland east coast, the southern Grand Bank and the Newfoundland west coast subdivisions, with areas between such as St. Pierre Bank and the Strait of Belle Isle being mixing areas of cod from adjacent subdivisions.

Marking experiments, meristic studies and *Porrocaecum* infestation studies conducted on cod in the eastern Newfoundland region, extending from Labrador to the northern part of the Grand Bank, would seem to indicate that the cod in this rather extensive region consist of a single, relatively homogeneous population. Topographic and hydrographic conditions are such that cod are not prevented from migrating from one end of this region to the other—in summer in the warm, shallow surface layer and in winter in the warm, deep layer of water. The entire

region is influenced by the cold portion of the Labrador Current and the cod increase in length and weight relatively slowly. However, the rate of increase in size of cod in Labrador sampling localities was found to be considerably slower than of cod to the south, off the east coast of Newfoundland. The cod were different, also, in other respects. The numbers which were sexually mature were significantly greater at the smaller sizes and younger ages in the Labrador region than in any other region of the entire Newfoundland area. A study of the otoliths revealed that in the Labrador cod, the deposition of the opaque layer on the otolith occurs much later in the year than in fish from other regions. Thus, cod from the Labrador region are sufficiently different from cod to the south to justify their being considered as a relatively distinct group. Though there is apparently no topographic or hydrographic barrier to prevent free movement of cod northwards and southwards, and though some Labrador cod do move to the east coast of Newfoundland, the migration is obviously of a small degree and distinct differences between cod from Labrador and regions to the south continue to exist.

In the region extending from the north of Newfoundland southward along the east coast to the northeastern part of the Grand Bank, tagging experiments have demonstrated considerable individual movement of cod along the east coast and between the northern part of the Grand Bank and the east coast; but most of the recaptures were close to the tagging point. Meristic studies indicated no significant differences between cod from various parts of this region. *Porrocaecum* infestation was of the same order throughout the region. The deposition of opaque growth on the otolith occurred at about the same period throughout the year, though a little later in the northern Grand Bank part of the region than in east coast localities. No significant difference was found in the age at which 50% of the cod were sexually mature throughout the region. Thus, on these bases, cod in the extensive region from northern Newfoundland to northeastern Grand Bank can be considered as another subdivision in the cod population of the Newfoundland area. However, it is obvious that complete intermingling does not occur within this eastern region, for the rate of growth of cod increases from north to south. It seems likely that incomplete intermingling is due to distance and not to the presence of bottom or temperature barriers.

Returns from tagging experiments conducted on the Grand Bank gave no evidence of inter-migration of cod between the southwestern part of the bank and the northeastern part. Vertebral averages indicated a distinct difference between cod from the two regions. The opaque layer of the otolith is deposited somewhat later in the season in the southwestern than in the northeastern Grand Bank cod. The southwestern Grand Bank cod generally lag behind the northeastern ones in reaching sexual maturity so that the incidence of mature cod is much lower at the smaller sizes and ages for the southwestern Grand Bank than for the northeast; the age at which 50% of the cod were mature was 7.5 years for the southwestern and 6.3 years for the northeastern Grand Bank in the samples examined. The average sizes for various age-groups of cod from the southwestern Grand Bank were generally much higher than for the corresponding

age-groups of the northeastern cod. Therefore, it seems reasonable to suggest that cod from the southern portion of the Grand Bank are separate and different from those to the north. It is most likely that the layer of Labrador Current water, with temperatures below 0°C, which is in contact with the northern, eastern and western edges of the Grand Bank at intermediate depths forms an effective barrier which prevents fish from the deeper waters of the northern area from mixing with fish of the shallower water on the body of the bank to the south.

Tagging experiments on the southern Grand Bank and on St. Pierre Bank have demonstrated some exchange between cod of these two regions and, in addition, a fairly widespread movement of cod tagged on St. Pierre Bank to various points along the south coast of Newfoundland, to the northern regions of the Grand Bank and even across the Laurentian Channel. Vertebral averages of cod samples from St. Pierre Bank were intermediate between the low averages on the southern part of the Grand Bank and the southwest coast of Newfoundland and the higher averages on the northern part of the Grand Bank. The average number of circuli in the first year of the scales was such that Thompson (1943) placed St. Pierre Bank cod in the same group as cod from the southern Grand Bank. Studies of *Porrocaecum* infestation showed cod from the northern part of St. Pierre Bank to have high infestations, of the same order as cod from the southwest coast of Newfoundland; on the southern part of St. Pierre Bank infestations were low, of the same order as the southern part of the Grand Bank. The deposition of the opaque zones of the otolith occurred at about the same time in St. Pierre Bank and southern Grand Bank cod, but began somewhat earlier in the Newfoundland southwest coast region. Sexually mature cod were found at smaller sizes in the St. Pierre Bank samples than in those from the southern Grand Bank, and, in this respect, resembled samples from the southwest coast. The age at which 50% of the cod in the samples were calculated to be mature was not significantly different at the 5% level from either the southwestern Grand Bank or southwest and west coasts of Newfoundland, though the coastal samples were significantly different in this respect from the southwestern Grand Bank. Very young cod of St. Pierre Bank increased in size at a slower rate than the southwest Grand Bank cod of similar ages and though from about the V-group onward the increase was at about the same rate for both regions, St. Pierre Bank cod were consistently smaller. The rate of increase in size of St. Pierre Bank cod was approximately the same at the younger ages as for the southwest coast cod, but greater at the older ages.

Thompson (1943) suggested that St. Pierre Bank harboured a rather "cosmopolitan" cod population, and was a sort of crossroads for migrating cod. The evidence outlined seems to support this, but indicates further that though St. Pierre Bank is a meeting place for many migratory cod from various surrounding regions, these fish do not mix completely on St. Pierre Bank and cod on the northern part of the bank resemble in many respects fish from the southwest coast of Newfoundland, whereas on the southern part of the bank the cod exhibit similarities to cod of the southern Grand Bank region.

Tagging experiments have shown a relationship between the cod of the west and southwest costs of Newfoundland. Results of meristic studies and *Porrocaecum* infestation counts are consistent with the existence of a single population of cod in the west and southwest coastal regions. The occurrence of the opaque zone at the otolith edge is apparently at the same time for both regions. All cod examined from both west and southwest regions were sexually mature at a 70 cm size, and the calculated age at which 50% of the cod were mature was not significantly different from one region to another. However, the increase in length and weight was somewhat more rapid for cod from the southwest coast than for the west coast. The southwest coast samples were taken in June after the migration of fish from the area to the west coast had occurred. It seems that the fish which do not join the schools migrating into the Gulf, but remain in the southwest coast region throughout the year, have somewhat better conditions for growth in length and weight than the migratory fish.

To the north, in the Strait of Belle Isle region, tagging has indicated that cod from outside the strait, from Labrador and the northern part of the east coast of Newfoundland, penetrate into the inner parts of the strait. This penetration is reflected in the gradually increasing cod vertebral averages from the northern part of the Newfoundland west coast to the Strait of Belle Isle. Cod of the Strait of Belle Isle samples apparently deposited the opaque zones at the otolith edge somewhat earlier than west coast samples and on this basis were closer in their resemblance to east coast cod. Strait of Belle Isle samples were intermediate between the east and west coast in the age at which 50% of the cod were sexually mature. In the younger age groups the rate of increase in length was almost coincident for Strait of Belle Isle and west coast cod; in older age-groups the Strait of Belle Isle and east coast cod were similar in this respect. This peculiarity is consistent with an inward seasonal migration into the northern part of the Gulf of older fish of the east coast area.

Factors causing differences between stocks. The existence of sub-divisions in the cod population of the area and the relatively small amount of intermingling of cod from different parts of the area explain in part why differences between regions in the various expressions of growth continue to exist. The reasons for the origin of these differences are not as well known. Among the environmental factors known to affect the development and growth of fish are temperature of the surrounding medium and amount and quality of food available (A. Dannevig, 1925, 1933; Fulton, 1904; Graham, 1929; Thompson, 1926; Winge, 1915).

Temperature can operate in two ways. Differences in temperature can result in differences in the food supply or can affect the appetite of the fish, decreasing the appetite at low temperatures, increasing it at higher temperatures. Fulton (1904), in experiments with various marine fish kept in tanks, believed that temperature was of first importance, acting directly on the metabolism of the fish and affecting the rapidity of their digestion. Fish would not take food when the water became very cold, because the ferments upon which the digestion depends acted either slowly or not at all. McKenzie (1934, 1938) conducted

feeding experiments on cod kept in tanks and found a definite relation between water temperature and the amount of food taken. The cod ate well at medium temperatures of their tolerance range and ceased eating entirely at very high and very low temperatures.

It is well known that variation in water temperature occurs in the Newfoundland area. General temperature differences have already been discussed. Although, because of hydrographic differences, water temperature conditions are not the same in all regions it is possible for cod from various parts of the area to be in water of approximately the same temperature by moving to the appropriate depth. But, for example, in warmer regions, acclimation to higher temperatures will probably result in cod actually occupying warmer temperatures.

In the area variation also occurs in food supply. In Labrador waters, examination of cod stomach contents generally revealed only small volumes of food, consisting mainly of such invertebrates as amphipods, spider crabs and pteropods. Fish food such as capelin, launce and herring does not seem to be available in large quantities in the Labrador region. In the Newfoundland coastal regions, however, large quantities of capelin, especially in the east coast region, and herring, especially in the west coast region, are eaten by cod. Farther offshore, in the bank areas, capelin, launce and other fishes such as young haddock and flounder are available and form an important part of cod food.

It was noted that in the oldest age-groups of cod in most regions there is a more rapid increase in size (Fig. 3 and 4). It is highly probable that some of this increase may be a result of these older and larger fish being able to obtain a more plentiful and nourishing food supply consisting of fish such as young cod, haddock, flounders and others.

Insofar as temperature and food supply are concerned, the Labrador environment is apparently not as favourable as other parts of the Newfoundland area. Therefore, the rapid attainment of sexual maturity in Labrador cod might be considered strange. However, the growth of the sexual products resulting in sexual maturity is as much an expression of growth as is increase in length and weight. Svärdson (1943) states that Alm in his work on trout in Sweden found instances where, in a favourable environment, not only was growth improved but maturity in relation to size and age was delayed. Alm (1959) reviews the work of many investigators on the connection between maturity, size and age in fishes. In his recapitulation Alm states, in part:

"For trout, char and whitefish a great number of investigators assert the occurrence of different forms or even species with different growth rate and different size and with different age at maturity. The small-sized forms are said to become mature rather early and have a rather short length of life, while the larger-sized forms reach maturity at a higher age and grow rather old. A similar condition is stated by some investigators to exist also in different populations of the same form or species of some cyprinids, sometimes also in perch and also in marine fish of both warmer and colder areas."

Alm reviewed the works of many investigators who were concerned with the factors that induce maturity and ripeness. Among these the work of Huitfeldt-Kaas on trout showed that lack of food tends to hasten the propagation of the

fish and increase the intensity of the reproductive process. Svärdson (1943) working with *Lebistes* found a positive correlation between weight of body and weight of male gonads except under conditions of very slow increase in body size when the correlation was changed so that the development of the gonad appeared faster. He found that with poor food supply spermatogenesis occurred in younger and smaller testes of *Lebistes*.

The results found in the Newfoundland area reveal that in cod from the southwest part of the Grand Bank, for example, growth in size is much more rapid than for the Labrador cod, yet the Grand Bank fish are generally not mature until a larger size and greater age than the Labrador fish.

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Keeping Quality of Pacific Coast Dogfish. II[1]

By B. A. Southcott, R. H. Moyer, E. G. Baker and H. L. A. Tarr

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ABSTRACT

Pacific coast dogfish (*Squalus suckleyi*) were stored in individual polyethylene bags at 0, 5 and 10°C; a control group of fish was iced. Viable bacterial counts, pH, ammonia and trimethylamine were determined daily. Pronounced ammoniacal odours were noted with only a few samples and were generally strongly masked by putrid odours.

INTRODUCTION

In the previous paper in this series (Moyer *et al.*, 1959) it was shown that Pacific coast dogfish, *Squalus suckleyi* (an elasmobranch), when handled in an ideal manner and stored fresh in a surplus of crushed ice or in refrigerated sea water at −1°C, spoiled no more rapidly than teleost fish previously studied at this Station. The present study was undertaken in an effort to determine whether or not the spoilage patterns usually reported for elasmobranch fishes would be encountered if the dogfish were handled under good-practice commercial conditions and held fresh at higher temperatures.

EXPERIMENTAL

Seventy-four fish were landed live at a commercial fishing plant and were beheaded, eviscerated and washed by experienced plant personnel. The fish were removed to the Station's laboratory immediately after washing and were randomly segregated into groups which were treated as follows:

24 fish iced (kept surrounded by a surplus of crushed ice throughout the storage period — ambient temperature 5 to 10°C)
24 fish placed in individual polyethylene bags stored at 0°C
18 fish placed in individual polyethylene bags stored at 5°C
8 fish placed in individual polyethylene bags stored at 10°C.

Two fillets were cut from a single fish from each treatment daily, skinned and used for bacteriological and chemical determinations. Precautions taken during skinning and filleting to minimize the transfer of organisms from skin surface to flesh or to subsequent samples included placing each fish on a clean sheet of kraft paper on a dry surface and using a clean knife for filleting; the fillet was then placed skin down on a clean sheet of paper and skinned in such a way that the fillet flesh was lifted off and placed in a clean plastic bag by a second operator.

Because of high storage temperatures involved in some instances, viable

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bacterial counts were made immediately after sampling with no prior incubation period. Modified artificial sea water was used to prepare agars and dilution blanks; the modified sea-water agar contained Bacto peptone, 0.4%; yeast extract, 0.1%; $FePO_4$, 0.001%; agar, 1.5%; dissolved in 80% strength modified artificial sea water (NaCl, 2.3%; $MgCl_2.6H_2O$, 1.1%; Na_2SO_4, 0.4%; KCl, 0.06%; $NaHCO_3$, 0.02%). An attempt was also made to provide a medium which would favour the development of any urea-decomposing organisms present. For this reason each sample was plated on three agars: modified artificial sea-water agar at pH 6.5 and 8.5, and modified artificial sea-water agar pH 8.5 containing 2.0% urea. The urea was separately sterilized and added to sterile melted and cooled agar just before the plates were poured.

Values for pH and volatile bases were determined as described in previous work (Moyer *et al.*, 1959).

RESULTS AND DISCUSSION

Figures 1 and 2 illustrate the changes in pH, volatile bases and viable bacterial counts under the four storage conditions.

The three points plotted daily represent viable bacterial counts using the three types of agar. The curves show gross changes in counts with particular reference to the type of agar used. Ammoniacal odours could be detected in only occasional samples of the dogfish and even less frequently on the agar containing urea; when such odour did occur on urea agar, it was very pronounced and never occurred on duplicate plates without added urea. The fact that the counts on any one day on the three agar media were almost identical and that ammoniacal odours occurred on only a few plates indicated that the total number of organisms was not influenced either by higher pH or presence of urea and also that an obligate urea-utilizing population was not established to the exclusion of other types.

The pH values and volatile bases in the iced samples were comparable to those previously found. In the samples stored at higher temperatures the volatile bases rose quite sharply at different times corresponding to temperatures of storage. Thus at 0°C a sharp increase occurred after about 13 days, at 5°C after 9 days, and at 10°C after 4 to 5 days, while with the iced fish this increase did not occur until after 20 days. The pH was generally higher at the higher temperatures and tended to rise with storage time. Values for volatile bases and pH of the samples stored in polyethylene bags were quite scattered. This situation had been anticipated since the individual fish were isolated from one another in separate bags. Less ammonia and trimethylamine were produced in iced fish samples than in bagged fish samples at 0°C, although bacterial counts in the two treatments were comparable. This may have been due in part to the leaching action of the water from the melting ice. Ammonia production exceeded 200 mg% in only one sample (15 days in bag at 0°C). This sample was also quite putrid. In general, putrid odours developed at the same time as ammoniacal odours and tended to mask the latter to a considerable extent.

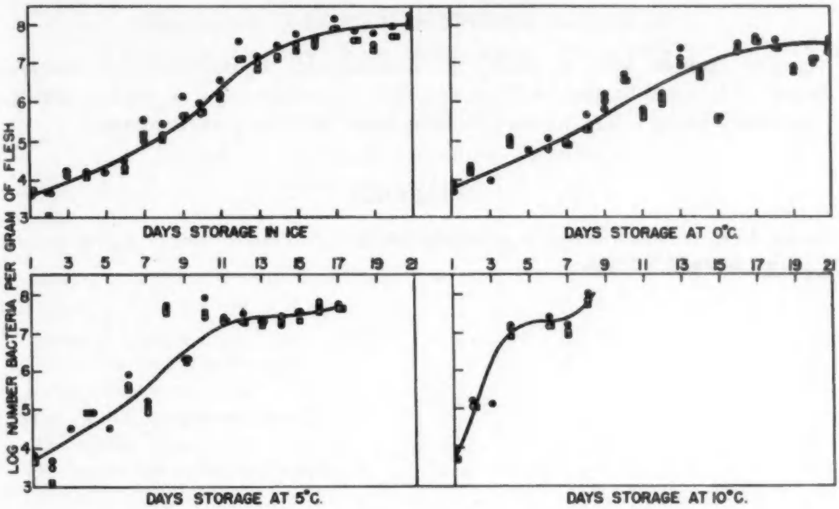

FIG. 1. Effect of storage in ice and in polyethylene bags at three different temperatures on the total viable bacterial counts of dogfish muscle.

Sea water agar; pH 6.5 — ●; pH 8.5 — ○; pH 8.5 + 2% urea — □.

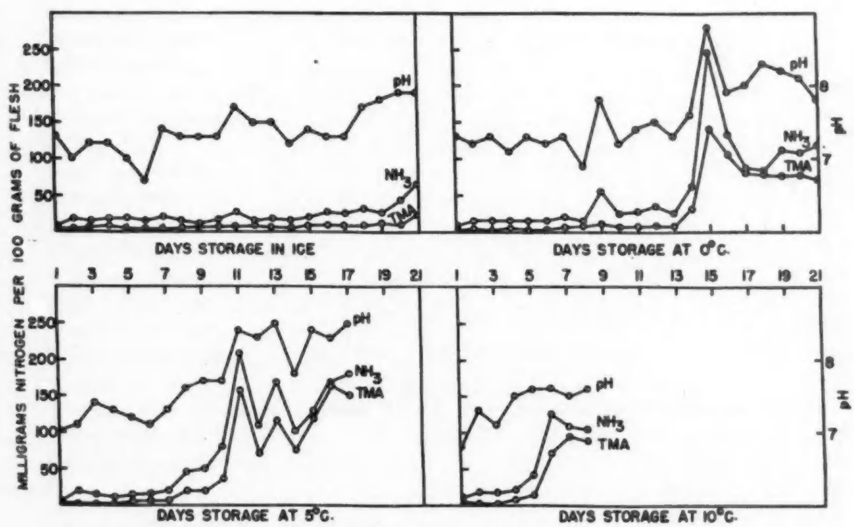

FIG. 2. Effect of storage in ice and in polyethylene bags at three different temperatures on the ammonium and trimethylamine content of dogfish muscle.

ACKNOWLEDGMENT

The authors wish to thank the investigators at the Fisheries Research Board's Biological Station at Nanaimo, B.C., for supplying live dogfish, and the Canadian Fishing Company for providing plant facilities and personnel.

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Moyer, R. H., B. A. Southcott, E. G. Baker and H. L. A. Tarr. 1959. *J. Fish. Res. Bd. Canada*, **16**(6): 791–794.

Economic Study of the Herring Fishery of Charlotte County, New Brunswick, 1956-1957[1,2]

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CONTENTS

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ABSTRACT

This report presents the results of an economic survey of the herring fishery of Charlotte County, New Brunswick, conducted in 1957 and 1958. It contains: (a) a detailed account of the capital investment and income position of the fishermen who were engaged in the herring fishery during the years 1956 and 1957; (b) some evaluation of the economic effects which the construction of hydro-electric power dams in Passamaquoddy Bay would have on the herring fishery of the area.

Except for a small complement of men employed on purse seiners, draggers and a few other modernized fishing craft, the fishing activity of Charlotte County fishermen is largely confined to inshore operations. As a result, the primary fishing industry is not highly capitalized. Average net incomes are also low compared with those prevailing in other industries, even with those derived from a number of fisheries elsewhere in the Maritime Provinces. Incomes from the weir fishery are particularly uncertain, in view of the wide fluctuation in yearly catches and the high, rigid operating costs. In contrast with weir fishing, purse seining has proven to be an efficient method of fishing in the region, and holds considerable promise for the improvement of earnings in the herring fishery.

It is expected that the construction of the proposed power dams would add to the cost of maintaining and operating weirs in Passamaquoddy Bay, thereby reducing returns to owners and fishermen in this segment of the industry. In view of the low earnings now derived from weir fishing in certain sections of the area, it is likely that a number of weir owners would not continue to maintain their weir investments if the power dams were built.

INTRODUCTION

Terms of Reference

In October, 1956, the International Joint Commission established an International Passamaquoddy Fisheries Board to study the effects which the construction, maintenance and operation of hydro-electric power structures in Passamaquoddy Bay would have on the fisheries of the region. The Board then appointed a committee, composed of Canadian and United States scientists, to plan and implement the necessary fisheries research.

In the early stages of investigation, it became apparent that an economic assessment would have to be made of any change brought upon the fisheries of the region by the proposed project. The Board, therefore, (in January 1957) requested the Federal Department of Fisheries to study the economics of the Canadian weir fishery. Subsequently, the Department expanded its study to cover the operations of Canadian herring purse seiners and herring carriers.

In May 1958, W. F. Doucet, Chief of the Economics Service of the Department of Fisheries in the Maritimes Area, was appointed to the Research Committee of the International Passamaquoddy Fisheries Board. His responsibility was to advise the Committee on the economic questions before them and to conduct such studies and investigations as might be necessary for the purposes of the Committee's work.

Nature and Area of Investigation

The economic study of the herring fishery of the Passamaquoddy region was begun in October 1957 and concluded in February 1959. Its purpose was twofold: (a) to assess the investment and income position of fishermen engaged

in the herring fishery, including those engaged in the herring carrier trade; (b) to determine the capital investment and manufacturing costs of the fish-processing industry. This was to serve as a basis for evaluating the economic impact of the construction of power dams on the fisheries of the region.

Special emphasis was placed upon the weir fishery, not only because of its importance to the economy of the region, but also due to the decentralized nature of the investment involved. Since weirs are stationary structures and spread throughout the area of investigation, detailed knowledge of investment and income by areas—as well as the determinants of their variations—was deemed a prerequisite to an economic assessment of any change in fish availability resulting from the proposed project.

All investigations of the primary fisheries were conducted on a sample basis. Except for the purse seining fishery, where data were only provided for the year 1957, the information obtained on fishing operations covered the two years 1956 and 1957. The area of study was Charlotte County.

The study of the operations of the secondary industry (fish processing) entailed a complete coverage of fish processors from Black's Harbour to the international boundary, excluding Grand Manan. Most of the firms interviewed provided information in considerable detail on their capital investments and their manufacturing costs; and some also submitted data on net earnings. All this information was obtained on a confidential basis.

Since the fish processing industry in the area of study is composed of a limited number of firms—with the main fish products processed by a few firms enjoying a more or less monopolistic position—a presentation of the industry's investment–income status could not be made without revealing the identity of individuals. These data, therefore, had to be withheld from the present report. The treatment was confined to a summary consideration of the industry's importance to the economy of the area, in terms of the overall capital investment it maintains and the employment it generates.

Acknowledgments

The investigation of the herring weir and purse-seining fisheries was organized by Mr D. R. Buchanan, staff economist of the Economics Service of the Department of Fisheries at Ottawa, under the direction of Dr D. W. Carr of that Service. He also completed the necessary field work, with the assistance of Messrs J. A. D'Andrea of the Maritimes Area office, Department of Fisheries, and A. Brown and W. Holt of the Fisheries Research Board of Canada Biological Station, St. Andrews.

In April 1958, Mr Buchanan left the service of the Department of Fisheries and W. F. Doucet assumed the responsibility for completion of the studies already begun, as well as for the organization and pursuit of other investigations discussed later in this report.

Thanks must be extended first to the many fishermen and officials of the fish-processing companies in the area surveyed who supplied the information which made this report possible.

The course and conduct of data collecting operations were greatly facilitated by the assistance and guidance provided by personnel of the Biological Station at St. Andrews, for which acknowledgment is gratefully made.

The Department's District Protection Officer at St. Andrews, Mr O. A. Rigby (now retired), and the fisheries officers under his supervision provided a good deal of historical data on the weir fishery. They also provided information on methods of fishing in the area which was most helpful.

Finally, thanks must be extended to a number of employees of the Department of Fisheries at Halifax and Ottawa who contributed in various ways to the preparation of this report.

PHYSICAL AND ECONOMIC SETTING

Description of the Area

Charlotte County, New Brunswick, is situated in the northwest extremity of the Bay of Fundy, bounded on the east by Saint John County and on the west by the state of Maine, U.S.A. It is an area of rolling and forested terrain, with an indented coastline of bays, inlets, estuaries and islands. Fishing is the principal primary industry. The landed area has a comparatively thick cover of forest, which provides a resource for a small supplementary industry, although the land itself is not suitable for a prosperous agriculture.

The county is a natural composite of four main geographical divisions. Of these, three are islands—Deer, Campobello and Grand Manan—whose residents are almost exclusively dependent for their living upon the resources of the sea. The fourth division is the mainland, the coastal fringes of which hem in the sheltered and herring-populated waters of Passamaquoddy Bay. Here the residents live in a mixed economy based on fishing, farming and lumbering. Numerous small islands are also strewn along the county coastline, and to the east and southeast of Deer Island. While these contribute little to the economic well-being of the inhabitants of the county, they lend much colour and beauty to the region.

Deer and Campobello Islands are at the entrance of Passamaquoddy Bay. Their presence protects the fishermen operating within Passamaquoddy Bay from the rough, open waters of the Bay of Fundy. Grand Manan, the largest island in the area, lies to the southeast at the mouth of the Bay of Fundy.

Passamaquoddy Bay, like the Bay of Fundy itself, is known principally for its geographical features and tidal ranges. Whatever the causal relationship between these may be, the Bay is the source of an abundant herring fishery. The sheltered nature of the Bay, along with the islands which enclose it, the cool saline waters and the behaviour of the tides also provide a suitable environment for the impounding of lobsters; and a prosperous industry is now based upon this activity in the area.

The main geographical features of Charlotte County are shown in Fig. 1. The Quoddy Region is designated by the broken double line. Lighter single broken lines represent boundaries of the statistical districts used by the Department of Fisheries.

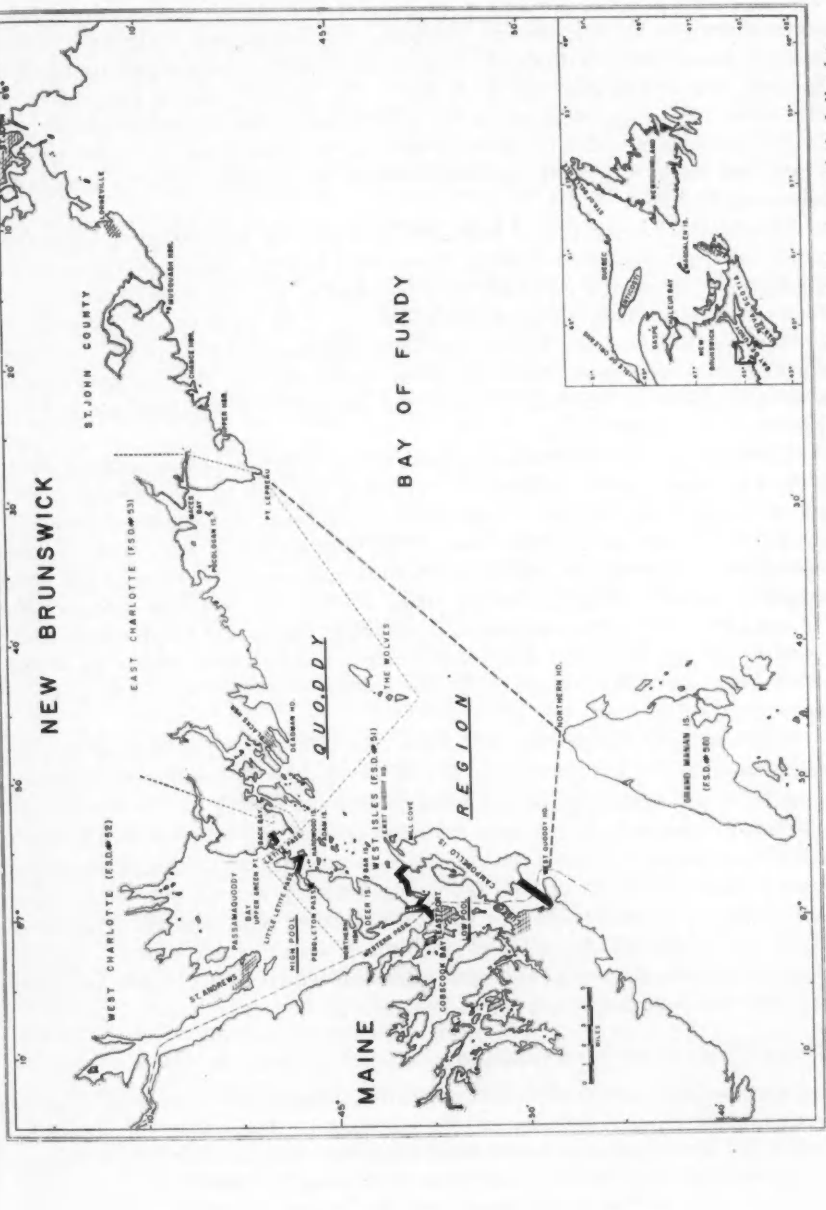

FIG. 1. Map of Charlotte County showing the Quoddy region, main population centres, and fisheries statistical districts.

Population and Industrial Composite

The principal concentrations of population in Charlotte County are in the urban centres of St. Stephen, St. Andrews, St. George and Milltown. There are a number of centres with smaller clusters of residents, among which are Black's Harbour, Beaver Harbour and Back Bay. The majority of the people live in rural areas. Farming, however, is the cocupation of but a small proportion of the rural population—about 1,900 in 1956—so that there is a considerable spread of residents along the county's shoreline and on the islands of Deer, Campobello and Grand Manan.

During the 75-year period from 1881 to 1956, the population of Charlotte County fell from 26,078 to 24,497. From 1951 to 1956, the most recent intercensal period, the county lost 2.5% of its population, with the main decline in the urban communities of St. Stephen and Milltown. The rural population suffered only a slight diminution. During the same period, the towns of St. Andrews and St. George experienced slight increases in population. While these changes were taking place in Charlotte County, the population of the province of New Brunswick increased by 8%.

Considerable difficulty is encountered in any effort to obtain accurate data on the Charlotte County labour force for 1957, the year of the fisheries study. However, a useful breakdown by industries can be found in a report by Grasberg and Whalen (1958, pp. 95–109). For 1956, they estimated the county labour force to be 8,160 persons, 7,660 of whom were employed. Of these, 2,107 were engaged in manufacturing, 2,700 in tertiary employment (services, government, etc.) and 2,853 in primary employment (agriculture, fishing and woods operations). According to the Dominion Bureau of Statistics, 1,863 were employed in the primary fishery in 1955 and, by 1957, the number of fishermen had dropped to 1,344.

Grasberg and Whalen also estimated that fish and other food processing combined accounted for more than 50% of the number of persons employed in manufacturing. The estimate was made before the closing of the textile mill at Milltown, which employed more than 500 people; and an allowance for this occurrence would serve to raise the proportion of total manufacturing employment currently attributable to the fish-processing industry to well over 50%. The value added by manufacturing in Charlotte County approximated $6,100,000 in 1955, and $3,500,000 was paid in salaries and wages in this sector. For the fish-processing industry alone, the value added amounted to $2,500,000, of which $1,100,000 was paid out in salaries and wages.

Fisheries Employment and Income

From the brief note above on the industrial composite of Charlotte County, the importance of the fisheries to the economy of the county is apparent. Historically, herring has been the most important species, although in recent years groundfish and lobsters have been increasing in importance. In 1957, the landed value of fish in the county was $1,700,000, about 25% of the gross

value of landings in the province of New Brunswick. The year 1948, when landings were valued at $3,000,000, represents the peak so far. Since that date, there has been a downward trend, which parallels the trend in herring landings.

Considering the 21-year period 1937–1957, and comparing the landings during the first four years of that period with those during the last four, the relative position of groundfish changed from 10.1% to 18.1%, that of lobsters from 11.5% to 27.9% and that of herring from 71.3% to 44.6% of the total value landed. The rise in the economic importance of lobsters and groundfish was principally a price phenomenon. During the same period, clams dropped to a place of insignificance in total landings—6.2% in 1957—a drop attributed to diminishing stocks.

The story of employment in the primary fishing industry of Charlotte County is also one of decline, but a decline that was accompanied by an increase in the physical output per man. In 1957, 1,344 persons landed more fish than about twice as many men landed in the year immediately prior to 1939. The herring fishery probably experienced the same rate of decrease in employment as occurred in general throughout the fisheries of the county. These data are not readily available, since statistics on employment in the herring fishery have only been reported separately in very recent years. Estimates can be made, however, and a close scrutiny of the statistics available for 1956 and 1957 reveals that the number of men fishing herring during those two years was closely related to the number of men fishing on motor, sail and row boats. Using this as a benchmark, it appears that the number of men prosecuting the herring fishery in 1957 was about 30% of the number so employed in 1937.

During the period 1937–1957, in which there was a decline in the labour force, there was a marked increase in the capital invested in the primary fishing industry of Charlotte County. The investment in vessels and fishing gear in the county increased from $1,100,000 to $3,800,000. The further extension of newer methods of fishing, especially purse seining (discussed later in this report), no doubt would lead to a further reduction in the labour force engaged in the herring fishery, without any diminution in output.

Fisheries Development in the Passamaquoddy Region

Herring fishing in the Bay of Fundy appears to go back to the earliest settlement in that region. The use of weirs for catching herring was known to the Acadian French who first settled in Nova Scotia, and was adopted in Passamaquoddy Bay about 1820. It was an effective way of catching fish before the introduction of the more active methods (purse seining and dragging for example), and was naturally adaptable to local conditions—the tidal rise and fall placing weirs in deep water and far from shore at high tide, and making them easily emptied at low tide.

The adoption of the weir in Charlotte County progressed slowly up to 1850. In that year, there were 60 weirs in the county—27 at Grand Manan, 21 at Campobello and 12 in the inner part of the bay. Canadian and U.S. fishermen took

an estimated 10 million lb of herring from Passamaquoddy Bay that year. In 1946, 109 million lb were landed, probably the highest herring landings ever recorded from Charlotte County waters. The number of weirs then operating in the County was 330. The number at Grand Manan and Campobello had hardly changed since 1850, which left over 250 distributed over the inner reaches of Passamaquoddy Bay (Huntsman, 1953).

The herring carrier appears to have been in operation from the early development of the industry, likely because of the dispersed nature of fish catching and the centralized nature of processing. Developments in the carrying fleet were followed by further developments in the weir fishery. The introduction of the steam packer in 1899 was followed by an increase in the number of weirs, because they could be operated profitably at greater distances from the processing plant then in operation at Eastport, Maine. The largest number of weirs in operation in Charlotte County was reached in 1919, when 507 were counted. The number had dropped to 280 by 1957.

The processing industry was an entirely different operation in 1850 from what it became in later years. From the 1850 herring catch, 10,000 barrels were salted and 70,000 boxes were smoked in Charlotte County. Those were large herring. In 1946, which was a phenomenal year for Charlotte County herring fishermen, over 71 million lb were exported fresh to Maine. The remainder was utilized for the production of 725 thousand cases of canned fish (sardines, snacks, etc.), 3,000,000 lb of smoked herring, 3300 barrels of pickled herring, 311,000 lb of vinegar-cured herring fillets, 11,000 barrels of bait, 48,000 barrels of oil and 2,500,000 lb of scales for pearl-essence manufacture (Huntsman, 1953).

A first attempt at sardine canning was made by George Burnham of Eastport, Maine, in 1867. He observed the canning of small pilchards in France, and conceived the idea of treating small herring in the same way. It was not until 1875 that sufficient success had been achieved to attempt a commercial canning operation, which also took place at Eastport. It failed; but an interest had been engendered which was eventually to grow. Around 1885, two Canadian fishermen, Lewis and Patrick Connors, began canning sardines at Black's Harbour, and the name Connors is perpetuated in the principal sardine canning establishment at Black's Harbour. By 1900, there were 5 canneries in Charlotte County and 79 in Maine.

The sardine processing industry of Charlotte County has always been restricted to a few firms. The highest number recorded was seven between 1916 and 1917. At the end of 1957, there was only one firm in the herring canning business, although it had a number of subsidiary companies and, of these, one comprised three manufacturing units. In all, then, there were five plants packing sardines in Charlotte County in 1957: two at Black's Harbour, one at Beaver Harbour, one at Back Bay and another at Fairhaven on Deer Island.

The herring fishery has always been the main basis of fish processing in Charlotte County. Nevertheless, other species have supported processing establishments. In 1957, there were three firms engaged in clam processing. Two of these, one at Pocologan and the other at Chamcook, operated canning factories. The third firm, located at Little Lepreau, was engaged in shucking operations. However, the clam processing industry of Charlotte County had been suffering declining fortunes since 1951, when clam landings reached approximately 900,000 lb. In 1957, landings had dropped to 123,000 lb. In consequence, a number of clam factories were compelled to cease operation.

The high tides and cold water of the Bay of Fundy have made some places in Passamaquoddy Bay and Grand Manan ideal locations for impounding lobsters. The great tidal amplitude provides a flushing mechanism for cleaning out pounds, while the cold water slows down the physical activity of the lobster, thereby reducing waste and damage from body contact in a crowded habitat.

There is some evidence that the origin of lobster pounds in Charlotte County predates 1920. Reference is made to a small operation there in 1916–17 (Annual Report of the Fisheries Branch, Department of the Naval Service, Ottawa, 1916–17, p. 2). In Maine, U.S.A., lobster impounding was already on a large scale at that time.

Development in the groundfish fishery had a late beginning. Until the late 1940's, this fishery consisted of a relatively small inshore operation from which salted fish was the principal product derived. Then, fishermen began to acquire larger and more highly mechanized fishing vessels (longliners and draggers), as they had done some years previously in several other sections of the Maritimes. This was followed by fresh fish processing, first on a small scale, but culminating in 1957 in the opening of a large, modern filleting and freezing plant at Beaver Harbour.

The modernization of vessels for the groundfish fishery is receiving considerable support and encouragement from the Government. This, combined with the availability of efficient facilities for the processing of fresh and frozen fish, should result in further development of the fishery.

Prices to Fishermen

A peculiar characteristic of the price of herring in the Passamaquoddy region is its apparent stability. However, this was not always the case and fishermen at various times endeavoured, with little success, to improve their bargaining position. The first recorded attempt to establish a basis for negotiating herring prices occurred in 1906, when a Weir Fishermen's Union was formed. It was the outgrowth of the following circumstance. Weirman had a successful year in 1905, but canning operators who, for the first time, used machines for making and sealing cans had full warehouses at the beginning of 1906. The canners in Maine agreed collectively to restrict output and to purchase only a

limited number of "hogsheads" (1 hogshead equals 1,225 lb) from fishermen per week. With plenty of fish and a restricted market, the price was forced down. In this situation, the Weir Fishermen's Union attempted to fix the price of herring at $8 per hogshead.

In 1907, weir fishermen began to disagree among themselves as to what the price of herring should be, and finally a separate organization was formed on Deer Island to act independently. This served to destroy the Union's cohesiveness, as well as to curb the general discipline needed to maintain an agreed price. The net result was the lapse of effort toward price negotiation.

There was a revival of union activity in 1924. In that year, U.S. canners, who were still in a dominant position, reduced the price of herring obtained from New Brunswick weir-men from $12 to $6 per hogshead. A general meeting of fishermen was called, and an agreement was reached not to export herring unless a price of $10 per hogshead was received. This resolution was given greater effect by the inclusion of a clause in the weir license which made its retention dependent upon compliance with the agreement. As a result, fishermen received nearly $170,000 more for their fish in 1924 (Annual Report of the Fisheries Branch, Department of the Naval Service, Ottawa, 1924–25, p. 32).

The following year, some fishermen began to sell below the agreed price. A number of weir licenses were cancelled, but the practice continued notwithstanding, with the result that only those who sold below the stipulated price of $10 could dispose of their fish. Because of this malpractice, the use of licensing to enforce a minimum export price was dropped in 1926.

While low prices have commonly prevailed in the herring fishery they have also, on occasion, reached unusual heights. At the beginning of 1938, for instance, prices ranged from $5 to $9 per hogshead. Catches were low that year and, in the competition for fish, prices were bid up to the unprecedented level of $53 per hogshead before the season ended. By contrast, the period 1941–1957 was one of remarkably stable prices. Average prices to fishermen during these years varied from 0.98¢ to 1.5¢ per lb, that is, within a range of 0.5¢.

The use to which fresh herring is put has always served as a basis for a price differential. Herring destined for human consumption, for instance, fetches a higher price than that which is used for pet food; and herring utilized for meal or fertilizer production sells for a lower price still. The quality of the fish when it reaches the processing plant largely dictates its end use and, by the same token, the price which the fisherman receives. Among the many factors which can affect the quality of herring, two are particularly important: (a) the intestinal content of the fish ("feedy fish", so-called, is unsuitable for human food production); (b) the type and grade of salt which is used as a preservative.

As far as lobsters, clams and other species in the Passamaquoddy region are concerned, they have never given rise to the price problems which have been characteristic of the herring fishery. Their relative scarcity has minimized the difficulties of marketing and assured a fair measure of reward to fishermen.

Market for Fishery Products

Lobster, which is now an important fish product of the Passamaquoddy region, is the highest priced sea food produced in the Maritime Provinces. It is transported alive to most of the principal urban centres of North America and appears, often as the most expensive item, on the menus of fashionable restaurants in Canada and the United States. Small quantities are at times flown to England and Europe.

Lobster is also marketed in other forms—principally in the canned state and as fresh or frozen meat—but in all cases it is a luxury food item. Except for canned lobsters including paste and tomalley, which are sold in appreciable quantities in England, the lobster products of the Passamaquoddy region find disposition on the North American market.

The herring fishery does not operate under such propitious market conditions. The canned sardine is in greatest demand where it serves as a low priced food. Its chief markets in 1957, as an item of human food, were in the low income countries of the Caribbean and in the colonial territories of Africa and Asia. Small quantities were sold in Australia and New Zealand.

Other herring products of importance are fish meal, fertilizer and pet food. the latter is a product of American plants and its sale is not a matter of concern to firms in Charlotte County. The markets for meal and fertilizer are found principally in North America and Europe.

The remaining fishery products of the region—clams, scallops, groundfish, etc.—are sold for the most part domestically and in the eastern United States.

Methods of Fishing Herring

Weirs. Weirs, or trap-like structures of posts or stakes, brush and netting, are the prevalent type of stationary gear used to catch herring in the Bay of Fundy. They are located along the shores of the Bay and in the inner coves, inlets, bays and estuaries.

The prospective weir builder must take many factors into account in selecting a site and positioning a weir. Among these are the availability of fish, the contours of the shore, the slope of the land beyond low water mark, the condition of the ocean floor, the tidal amplitudes and the direction and strength of tidal currents.

Once the site is selected, a skeletal structure is erected—usually heart-shaped and resembling a corral (Fig. 2). This structure consists of posts or stakes driven into the ocean bottom, at distances of approximately 6 feet. The stakes are securely tied together by two rows of ribbands, i.e., smaller posts or stringers spiked horizontally to the stakes. The bottom ribbands are spiked to the stakes at low water level, with the top ribbands positioned about 3 feet higher. The stakes extend a foot or so above the top ribbands and, since they are completely

submerged, top or marline poles are spiked to these extensions. When the skeletal structure is covered with brush, racks (prefabricated brush panels lashed to the lower portion of the weir) and netting, the weir is ready for fishing.

Weirs vary in design and form, depending upon the physical characteristics of their location. Nevertheless, they consist essentially of a pocket or trap (heart) and one or more fences or leaders extending from the weir mouth to the shore line (Fig. 2). In some cases, pounds (extra pockets or holding units) are also fitted to the trap.

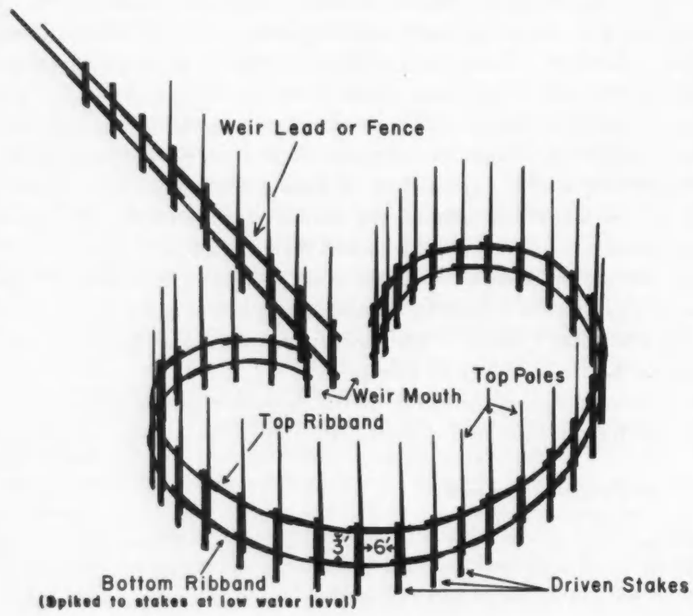

FIG. 2. Skeletal weir structure.

A carrier and usually a pumper, attended by two or three small boats equipped with a purse-seine, are used to fish a weir (Fig. 3). The pumper and the small boats (one may be powered) enter the weir, close the mouth and run the seine around the inside until the two ends are brought together and the catch completely encircled. When the seine is pursed up and the herring gathered within it, the net is gradually hauled in, enclosing the fish in but a small portion of it. The carrier then usually enters the weir, and the catch is pumped into its hold. If a pumper is not available, the fish may be dipped directly from the net into the hold of the carrier, or the catch may be gathered into small boats and then transferred to a carrier.

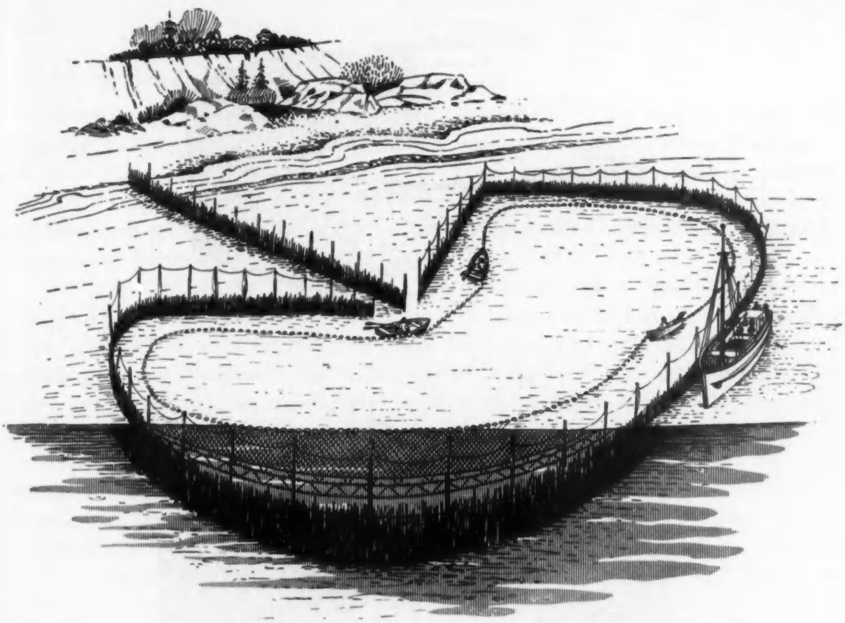

FIG. 3. An Atlantic coast sardine weir.

PURSE SEINES. Large quantities of herring are taken in seine nets operated mechanically from powered fishing craft. These craft are a type of "Cape Island" boat, ranging in length from 35 to 60 feet.

The size of the seine used is governed by regulation. The length varies from 100 to 200 fathoms, the depth at the bunt from 120 to 150 feet and the depth at the ends from 70 to 90 feet. It is rigged like a gill net, with floats threaded on the head-line, and the bottom is kept submerged to the fullest possible extent by weights attached to a rope (lead line) connected to the foot of the seine. It also has a rope (purse line) threaded through rings along the lead line, with which to "purse up" or close the bottom of the seine. The larger Atlantic purse seiners employ nets that are made completely of nylon, except for the brass rings that also serve as weights.

When a school of fish is located, the seiner, accompanied by a carrier and a pumper, moves into position and launches a skiff or rowboat to which one end of the siene is attached (Fig. 4A). The parent craft encircles the fish, with the net running out over the side, and joins up with the skiff, thus bringing both ends of the seine together (Fig. 4B). The two ends of the net and the purse line are then brought aboard the vessel. By means of power winches, the bottom of the net is closed or "pursed" and the mesh is hauled in until the fish are enclosed in a small portion of it (Fig. 4C). The pumper and carrier move into position, and the catch is pumped into the carrier's hold. Small seiners often use dip nets to transfer fish from the net to the holds of carriers.

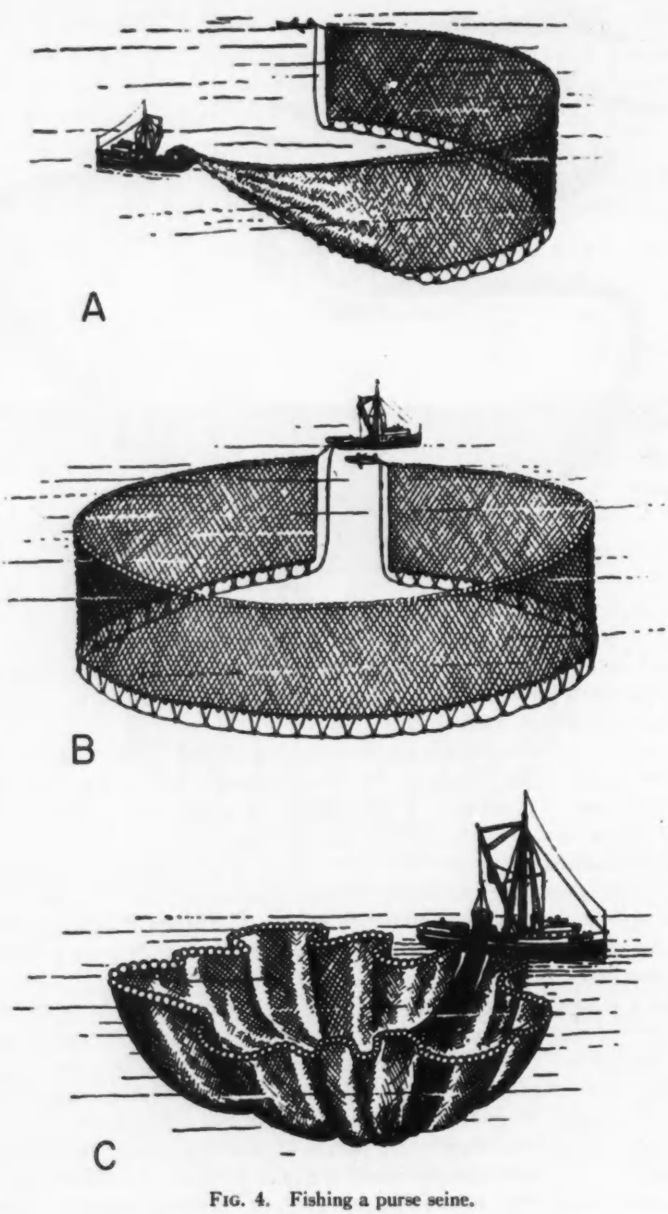

FIG. 4. Fishing a purse seine.

THE WEIR FISHERY, 1956 AND 1957

Nature of Weir Fishery

Weir personnel—their occupational status. The weir, as a method of fishing, has been employed by herring fishermen on the eastern Atlantic seaboard for more than a century. Its history is characterized by the relative absence of change in either technology or business organization. Its future would seem to depend upon the extent to which fishermen will continue to resist technological change and, hence, the substitution of capital for labour.

As is true of many fisheries of the Canadian east coast, the weir fishery is intensive in its use of labour. Moreover, a large proportion of the "working force" engaged in weir fishing consists of fishermen who have neither equity in fishing gear and equipment nor a guaranteed wage for the services they render. They are tendermen, so called, who tend or operate fish weirs for a pre-determined share of the season's catch.

There is another feature of the weir fishery which stands out in any consideration of personnel organization or distribution of returns in weir fishing. This is the prevalence of one class of owners who, for the most part, do not participate actively in weir operations. No exact parallel exists in other fisheries of the Atlantic region. They are typical investors in the modern corporate sense since, with few exceptions, their sole contribution to the enterprise is represented by their share of ownership. As can be seen from Table I, more than 43% of the owners of 127 weir enterprises in 1957 were in this class.

The personnel associated with weir fishing can be divided into three groups. The first is composed of non-tending owners—investors who, for the most part, exercise little or no proprietary control and do not participate actively in weir fishing. The second consists of tending owners, who either manage the weir enterprise or assist with actual fish-catching operations. In the last group are the tendermen, those who are hired to tend the weir. The second and third groups constitute the "working force" of the weir fishery.

The distribution of capital equity among this personnel, as well as the degree of labour utilization in weir fishing, may be derived from an examination of 127 weir enterprises that participated in the herring fishery in 1957. These enterprises operated 166 weirs, that is, 60% of all weirs in operation in the area surveyed in that year.

Table I. Persons associated with 127 enterprises (166 weirs) in operation in 1957.

Occupational status	Number	Percentage of total
Tending owners	191	39.0
Non-tending owners	142	29.0
Sub-total	333	68.0
Hired tendermen (non-owning)	156	32.0
Total	489	100.0

While there were 489 men associated with these enterprises in 1957, the active working force consisted of 347 men; and of the latter, only 55% had an equity in weir capital.

An analysis of the personnel composition of the typical weir enterprise must, however, be undertaken from another direction. Many weir fishermen are associated with more than one enterprise—for example, some who are owners pure and simple in one enterprise may be tending owners or hired tendermen in others—so that, when the fishery is examined in terms of its organizational units, inter-unit duplication of personnel must be recognized.

The summation of the number of individuals reported by each weir enterprise is given in Table II.

TABLE II. Personnel composition of 127 weir enterprises, 1957.

Personnel	Number	Percentage of total
Tending owners	229	33.2
Non-tending owners	227	32.9
Sub-total	456	66.1
Hired tendermen (non-owning)	234	33.9
Total	690	100.0

From this it can be seen that the average personnel per weir enterprise numbered 5.4 men. The labour complement (463) averaged 3.6 men, while the owner class, not represented in tending operations, averaged 1.8 men. Over 50% (234) of the tendermen class consisted of hired labour.

AGE COMPOSITION OF OWNERS. Attention was just drawn to the relatively high proportion of weir owners who stand aloof from weir operation, even from its management. Approximately 50% of all owners covered in this study were in this class, known locally as non-tending owners.

In a number of cases, weir owners in this class have alternative sources of income. This enables them to meet the uncertainties inherent in the weir fishery with greater ease—uncertainties imposed by seasons which seldom exceed 6 months, the yearly fluctuations in catches and the nature of investments in weir and associated equipment.,

There are, of course, a few fishing companies for which the weir fishery constitutes but one branch of a large fishery operation—where the weir enterprise is large (composed of several weirs) and part of an integrated business complex, and where risks and even losses are spread in a manner which permits their absorption with little discomfort. The typical weir enterprise, however, is small; and some of the owners are independent of weir receipts, not because of success in other branches of the fisheries, but because they are well established in other pursuits or retired in relative affluence[4].

[4]This observation on the income position of owners is qualitative, being based upon general knowledge and opinions which the weir survey was not designed to confirm or deny.

Partial support for this observation is provided by data on the age of owners obtained during the weir survey. Of the 81 owners who declared their ages, 74% were over 50 years of age, with about 55% having passed the 60 mark. Only 21 men were under 50 years of age, of which one only was under 40. Ownership, therefore, was preponderantly in the hands of the "older set"—men who had either retired or were approaching retirement.

There are two fairly obvious reasons for the relative absence of young men in the weir ownership class. The first is that the returns from weir investments are not sufficiently rewarding to induce the application of new capital (Tables VIII to XV). The second is the diffculty of entry in the fishery, due to environmental and institutional factors.

Ownership and environmental rigidities. As indicated in an earlier section, weir fishing is an old fishery which has withstood the trials of time with virtually little change in either technology or organization. From the beginning it emerged as a decentralized fishery, and remains so today, with weirs scattered over a wide coastline and with the one-weir enterprise still constituting the typical business unit.

Within this environment and tradition, a substantial degree of vested interest developed among families and family groups—monopolistic in a narrow sense. This was principally due to the fact that weir privileges, which were granted by the Crown (as they still are today), bestowed exclusive operating rights to individuals at specific locations—rights which could be preserved indefinitely so long as weirs were built, at least every second year, on the sites approved by law. As an added safeguard against encroachment, the law provided (and still provides) that weirs be separated by a distance of at least 1,000 feet. Thus, individuals and families who obtained weir privileges tended to retain them regardless of fortune, for fear that if allowed to lapse they might never be recovered or else fall into undeserving hands[5].

The strength of family ties also contributed to this development in the weir fishery. As is true of most fishing regions in comparative isolation, life in the coastal sections of Charlotte County, particularly the islands, centred largely around the family and the means of livelihood by the sea; and as inshore fishermen in general prize the nearness of their homes to their means of livelihood, so did weir fishermen seize upon weir locations which suited the established pattern of the home economy. The result, then, was a fishery characterized on the one hand by semi-monopolistic family and family group elements, and on the other hand, by the creation of small enterprises or business entities which each family unit could manage and control.

Our study, being economic rather than sociological, did not probe into the subject of family ties, inheritance and other related questions. For this reason, the discussion of family influence as it relates to concentration of ownership and

[5]All sites are not suitable for weir fishing. Suitability depends upon tidal conditions, water levels and other factors. As the fishery developed, weir sites became more and more marginal; and owners who found themselves established in favourable locations were inclined to perpetuate their ownership.

organization in the weir fishery is largely qualitative in nature, having as its main support the views of allegedly informed residents. Statistically, the only evidence at hand is provided by a classification of owners by family names, presented in the form of a frequency distribution (Table III).

TABLE III. Distribution of 119 surnames classified according to the number of weirs associated with each.

No. of weirs	No. of surnames
1	46
2	31
3	11
4	8
5	8
6	4
7	1
8	5
9	2
10	1
11	–
12	–
13	–
14	–
15	2
Total	119

As to the size of weir enterprises, the survey results were more conclusive. Of the 112 weir enterprises studied, 92 were 1-weir enterprises, 15 were 2-weir enterprises and 5 consisted of enterprises with 3 or more weirs. Moreover, of the 333 owners included, 293 had shares in 1-weir enterprises and 20 had shares in 2-weir enterprises, with the balance having ownership in 3 or more enterprises. Thus, the small enterprise unit, consisting of 1 weir, is represented as the typical business entity in the weir fishery.

The rigidities just described tend to restrict entry into the industry and, thus, to work against the forces of competition which normally prevail in the exploitation of a common property resource. Some are environmental restrictions —social and physical—but others, equally strong and effective, have their base in government regulations. They may be summarized as follows:

(a) The average enterprise is small, consisting of 1 weir, rendering it easy to manage and operate by the family group, friends or relatives.

(b) The privilege to operate a weir at a given location is granted by the Crown, but once obtained, and the prescribed conditions met, the recipient has a monopoly for as long as desired.

(c) Weir sites are also protected from outside encroachment by law, since all weirs must be separated by a distance of at least 1,000 feet.

(d) Owners are prone to perpetuate their ownership, since the legal cost of retaining a weir site is inconsequential ($1.00 per year), and their monopolistic position is assured.

(e) Only certain sections of the area under review are suited to weir fishing, due to oceanographic and other conditions. There is, therefore, a limit to the availability of sites, and most of the best ones have been claimed and are thus outside the open market.

The prevalence of such market impurities explains, at least in part, the poor representation of young fishermen in the weir ownership class. Barring acquisition of property or location through inheritance, entry into the weir fishery on one's own account is subject to impediments which, in some areas at least, are difficult to surmount. At the same time, there is evidence of a growing interest in purse seining, which is treated in a subsequent section of this report. Being a mobile and more capital intensive method of fishing, it offers opportunities for profit which are denied a stationary unit of gear such as the weir. However, there are restrictions at present—social and institutional—which still limit its attractiveness as a field of investment.

Sharing of receipts. As in all fisheries, the quantity of fish caught and the price it commands on the market are the leading determinants of income in the weir fishery. On the supply side, two factors also exert a paramount influence. The first is the availability of fish, as influenced by the weather and other natural conditions affecting fish movements, over which the weirman has no control. This is particularly significant in the case of stationary types of fish-catching equipment such as weirs. The second factor is the experience and skill of weir builders, in locating sites and positioning weirs thereon to provide the greatest opportunity for catching the fish frequenting these grounds.

The receipts derived from weir fishing are shared by a number of persons—non-tending owners, tending owners, and non-owning tendermen. With a few exceptions, a conventional sharing arrangement divides the proceeds from the catch (gross stock) equally between weir owners and tendermen in three of the four areas studied. These are the Mainland, Deer Island and Campobello Island. On Grand Manan Island, on the other hand, sharing arrangements exhibit considerable variations from one enterprise to another. On the average, about 70% of the gross stock goes to owners, 30% to tendermen.

The share of receipts accruing to the non-tending owner is determined solely by the amount of his investment. The tending owner shares in two ways: (a) in the gross stock claimed by owners, on the basis of equity; (b) in the gross stock allotted to tendermen, where all tendermen normally share equally. The returns to the non-owning tendermen are normally confined to a share of the gross stock allotted to tendermen. Only a relatively small proportion of non-owning tendermen—found principally on Grand Manan Island—are paid a stipulated money wage.

Most costs associated with building, maintaining, tending and fishing weirs are met by owners. The amount apportioned to each owner is governed by the

extent of his investment. Private agreement respecting financial responsibility are believed to exist, but these could not be determined from our survey.

The "share system" of labour remuneration just described prevails, in one form or another, in most primary fisheries—a wage system which has few parallels in other branches of economic activity. Its origin dates back to the days when fishing boats and gear were owned jointly by the crew; and it was undoubtedly devised as a means of relieving the owner of at least part of the risk and uncertainty attached to fishing, and to give the enterprise greater incentive and an added measure of flexibility (Turvey and Wiseman, 1957).

To the extent that risk sharing or spreading was a contributing factor to the adoption of the "share system", its prevalence in the weir fishery to this day has a ready explanation. For one thing, the quantity proceeds from a weir are highly dependent upon both the weather and the fish supply. Moreover, the average owner has normally a small capital investment which is localized, stationary, largely confined to the capture of one species and unsuitable for alternative uses. In these circumstances, the payment of a regular, fixed wage bill would often render weir operation unattractive or impossible after a number of poor, unlucky seasons. A share system of wage payment favours a larger degree of employment than other less flexible forms of remuneration.

As indicated by the preponderance of non-owning tendermen in the weir fishery (Table I), and the net income data given later in this report, the fisherman in this sphere of activity is largely insensitive to the lure of higher earnings—and most assuredly less uncertain returns—in many other sectors of the economy. At least this is so in the short run. The fact that the fishery is often prosecuted with friends or relatives, the incentive provided by the hope of a good catch, as well as other factors, all contribute to the individual's immobility. Of course, fishermen as a class are reputedly immobile. In the long run, however, the fisherman's returns from fishing must at least approximate his opportunity cost; like other workers, he will tend to seek those avenues of employment which will best reward his services.

Fishing Effort

Data obtained during our field investigations on the number of days weirmen are engaged in the various weir fishing activities are inconsistent and subject to a high degree of error.[1] In consequence, an accurate account cannot be rendered.

Activities preparatory to fishing operations. Activities preparatory to fishing operations normally begin during the winter months, when many weir operators, who own wood lots, cut and transport to the weir site the wooden material which will be needed for weir construction or repair. Then, early in the spring—before the herring "strike", but after crews have been assembled—weirs are inspected, adjusted, repaired and placed in complete readiness for fishing.

Unlike some capital assets, the operating efficiency of weirs can be seriously affected by normal wear and tear. Accordingly each spring, all weir parts that

have suffered damage or wear are repaired or replaced. Generally, about one-fifth to one-fourth of the stakes, ribbands and top poles and about one-half of the brush are subject to annual renewal. Only when such repairs have been effected can the webbing and racks be lashed to the structure and the weir placed in readiness for fishing.

In most years, additional preparatory work precedes catching operations. Often, a number of alterations are made: the weir may be moved to a new site; its mouth or entrance may be repositioned; or changes may be made to the number, length and direction of weir leads. Even extensions may be necessary such as, for instance, the construction of a "pound" or holding section, so that fish may be held without impeding catching operations. For all this work weirmen, especially tendermen, must give liberally of their labour.

The month of March generally signals the commencement of weir building operations. From a total of 145 weirs in 1957 for which building data were obtained, about 24%, 32% and 25% were reported as being built during the months of March, April, and May respectively. Two weirs only were reported under construction earlier.

As to the time spent in setting weirs in catching readiness, our recorded data indicate a period of 14 to 21 days. Many factors of course affect the time which may be required in any one year. Foremost among them are: the weather, always the arbiter of the fisherman's fortune; the availability of fishing crews and weir materials; and the number of men and weirs under the control of the weir manager.

Catching operations. As is true of workers in other fields of economic activity, weirmen exhibit varying degrees of application to the pursuit of their trade. For some, the more zealous, weir fishing begins in March and ends in November each year, which is the maximum fishing period possible because of the weather conditions which prevail in winter. For the majority of fishermen, however, the fishing season lasts for a period of 6 months, from May to October inclusive. In general, the number of months fishermen tend their weirs is governed by the availability of fish and the market demand, as well as by the opportunity for alternative employment.

Post-season work—weir dismantling. Once fishing operations cease, there remains the task of dismantling or "stripping" the weir, i.e., of removing the nets and racks, and often the brush from the fixed structure. This is commonly done in late October or early November, although some dismantling may be done as early as August or September, and as late as December. In all cases, the job must be completed before the onset of the more rigorous winter weather. Usually, little time is required to strip a weir, varying from 1 to 3 days.

Capital Investment

Owing to the relative absence of change in method of fishing, the proportions in which the agents of production have been applied in the weir fishery have

remained fairly constant since the beginning of this primitive industry[6]. Moreover, existing statistics show no positive relationship between the amount of investment in weir installations and operating income, so that there is little inducement for the weir owner to increase his investment in the weir fishing unit. It appears that the main determinant of the volume of capital investment in weirs is the change in the rate of egress from or entry into the fishery.

The values given in Table IV for weir materials represent the cost of replacement. Some items, such as stakes, poles, etc., are acquired by the fisherman without cost—except for the value of his own labour—and seldom enter the open

TABLE IV. Current value of the weir materials and associated weir gear of 86 weir enterprises (106 weirs) in 1957.

Item	Value	Percentage of total	Average per enterprise	Average per weir
	$		$	$
(a) Weir materials				
Stakes	109,430	22	1,272	1,032
Ribbands	18,546	4	216	175
Top poles	8,786	2	102	83
Rack legs	15,494	3	180	146
Rack band poles	24,644	5	287	232
Bottom brush	16,207	3	188	153
Top brush	10,131	2	118	96
Pier materials	17,681	4	206	167
Rope	7,647	1	89	72
Top nets	96,113	20	1,118	907
Bottom nets	92,933	19	1,081	877
Drop nets	10,126	2	118	96
Hardware	20,169	4	234	190
Pile-driving cost	42,442	9	494	400
Total	490,349	100	5,703	4,626
(b) Associated weir gear				
Motor boats	20,490	14	238	193
Other boats	15,854	11	184	150
Weir scows	8,347	6	97	79
Seine racks	1,475	1	17	14
Seine nets	30,711	21	357	290
Weir pile drivers	7,040	5	82	66
Herring purse seines	225	...	3	2
Herring shut-offs	14,460	10	168	136
Shore equipment	29,995	21	349	283
Miscellaneous	16,269	11	189	154
Total	144,866	100	1,684	1,367

(c) Total capital investment of 86 entrprises (106 weirs) = $635,215
Average per enterprise = 7,387
Average per weir = 5,993

[6]The substitution of capital for labour has been noticeably slow in most sectors of the fishing industry, compared with other sectors of the economy. However, the stationary method of fishing employed in the weir fishery has few parallels.

market. Similarly, there is a limited market for most used materials. For these reasons, the measurement of current market value is difficult and unrealistic. The figures given for boats and other associated gear represent current market value.

The enterprises whose capital investment is detailed in Table IV comprise three size categories: 1-weir enterprises, of which 72 are represented; 2-weir enterprises, which number 12; and enterprises consisting of 3 or more weirs, of which only 2 are represented. The capital investment in weirs and associated gear for these groups is given in Table V.

TABLE V. Capital investment by weir enterprise groups, 1957.

Enterprises	Number	Total investment	Average per enterprise	Average per weir
		$	$	$
1-weir	72	414,802	5,761	5,761
2-weir	12	133,602	11,133	5,567
3+-weir	2	86,811	43,405	8,681
Total	86	635,215	7,387	5,993

In view of the differences in oceanographic and topographic conditions within the region studied, weir construction (size of weir, amount and type of material used) exhibits certain variations among areas. This in turn is reflected in the average value of capital investment, as evidenced in Table VI.

TABLE VI. Average investment of 106 weirs by areas, 1957.

	Number of weirs	Weir material	Associated gear	Total
		$	$	$
(1) Inside proposed power dams				
Mainland	25	4,247	1,283	5,530
Deer Island	3	4,033	1,360	5,393
Campobello	7	4,479	816	5,295
Sub-total	35	4,275	1,196	5,471
(2) Outside proposed power dams				
Mainland	26	4,680	1,792	6,472
Deer Island	20	3,577	1,244	4,821
Campobello	2	5,830	1,140	6,970
Grand Manan	23	5,907	1,271	7,178
Sub-total	71	4,799	1,451	6,250
(3) Inside and outside dams				
Mainland	51	4,467	1,543	6,010
Deer Island	23	3,636	1,259	4,895
Campobello	9	4,779	888	5,667
Grand Manan	23	5,907	1,271	7,178
Total	106	4,626	1,367	5,993

It can be observed that substantial variations in average weir investment exist both within and among the separate areas of the Passamaquoddy region. For the region as a whole, the highest investment per weir prevails on the island of Grand Manan, which exceeds the regional average by about 17%. This arises principally from the value ascribed to weir material. Investment in gear associated with weir fishing, on the other hand, is below the overall average by about 7%. In contrast with Grand Manan, average weir investment on the mainland is virtually the same as the regional average, but investment in associated gear is substantially above that of any other area. Campobello and Deer Islands show the lowest average investment—Campobello Island lowest in associated gear, Deer Island lowest in weir material.

For a clearer understanding of these locational variations, attention must be drawn to the composition of weir investment in the four principal areas surveyed. This is provided in Table VII.

TABLE VII. Average weir investment by items and by areas, 1957.

	Mainland	Deer Island	Campobello	Grand Manan	Average
	$	$	$	$	$
Weir materials					
Stakes (driven)	1,150	524	1,328	1,165	1,032
Ribbands	168	158	283	166	175
Top poles	93	87	74	59	83
Rack legs	181	185	192	13	146
Rack band poles	255	375	317	6	232
Bottom brush	129	137	118	236	153
Top brush	84	68	114	142	96
Pier materials	28	664	47	24	167
Rope	59	43	57	129	72
Top nets	868	873	742	1,091	907
Bottom nets	728	58	669	2,107	877
Drop nets	74	94	115	137	96
Hardware	217	194	202	127	190
Pile-driving cost	433	176	521	505	400
Total	4,467	3,636	4,779	5,907	4,626
Associated gear					
Motor boats	189	225	188	174	193
Other boats	111	123	101	280	150
Weir scows	114	99	28	–	79
Seine racks	1	–	–	62	14
Seine nets	271	330	287	292	290
Weir pile drivers	107	43	56	4	66
Herring shut-offs	36	152	106	355	136
Shore equipment	465	199	77	43	283
Miscellaneous (netting, rope, etc.)	249	78	45	61	154
Herring purse seines	–	10	–	–	2
Total	1,543	1,259	888	1,271	1,367

The cost of weir materials constituted the major component of weir investment in 1957, being over 70% of total investment in each of the areas here examined. In this category, the major cost items were stakes, rack band poles, top and bottom nets and pile driving[7] which exhibited striking variations by areas.

While some allowance must be made for quality differences in weir material in the four areas considered, cost variations are more directly a function of the quantity of material used. Except for netting and rope, which of course vary in quality and price, weir material in general is fairly standard, leaving the user with little choice. The quantity of material, on the other hand, varies appreciably from location to location, since it is determined by the physical environment of the weir site—the depth of water and tidal amplitudes determining the size of stakes, poles and nets used, and the shore contours and paths of ocean currents determining the type of weir construction, length of leaders, etc. Investment in pier material, for instance, is particularly high on Deer Island. Due to the rocky nature of the terrain, weir stakes in many locations cannot be driven into the ocean floor. As a counter measure, pier-like structures (wooden flooring) are built, to which stakes are fastened, then sunk to the ocean bottom. This explains the low recorded investment in stakes on Deer Island, since a large segment of stake cost is included in pier material.

Apart from weir material, weir investment covers boats, seines, shore installations and other gear and equipment. To some extent, variations in investment in such items may arise from the fact that certain types of gear are best suited to particular areas such as, for instance, the high investment in herring shut-offs in Grand Manan. This notwithstanding, investment in auxiliary gear and appurtenances in most fisheries is largely determined by the individual's business sense and resourcefulness.

There is, however, one investment component in this category which warrants a closer examination. This is investment in shore installations, such as landing facilities, camps, sheds and other structures. In the area designated as the mainland, average investment in this item in 1957 was approximately one-third the average investment in all gear and equipment associated with weir fishing. In other areas, particularly Campobello and Grand Manan, shore equipment accounted for a small proportion of total investment in associated gear (9% in Campobello, 3% in Grand Manan). The explanation lies in the fact that a number of weir owners and operators on the mainland operate weirs at some considerable distance from their homes; and they need installations or structures near the weir site, not only to serve as living quarters, but to provide storage for weir equipment as well. On the islands, so-called, weirs are much closer at hand, so that fishermen can fish with relatively little travel from and to their homes. In consequence, few cottages or camps are needed and investment in storage sheds or other structures is quite low.

[7]This is truly a labour cost which should be incorporated in the value of stakes, nets and brush. However, since it could not be allocated with any degree of accuracy, it was treated as a separate item.

OWNERSHIP AND INDEBTEDNESS. Relative to other inshore fishing enterprises where the average capital investment is commonly low, capital ownership in the weir fishery is spread among many owners. In the lobster fishery, for example, an "own-account" fisherman in full and complete ownership of a boat, lobster traps and other fishing requisites is commonplace. This is not so in the weir fishery. The typical weir enterprise, except for a limited number of fishing firms, consists of a number of shareholders and, in many instances, at least one owner has shares in a number of weirs. Data obtained on 127 enterprises for 1957 revealed an average of 3.6 owners of share capital per weir enterprise (Table II).

Owing to this diffusion of ownership, with its consequent effect on the magnitude of individual proprietorship in the weir enterprise, capital indebtedness is of negligible significance in the weir fishery. Only 33 respondents reported capital debts in 1957. In total, the amount outstanding was calculated at only $49,421, a somewhat small proportion of the total value of weir capital in existence.

It should be remembered, however, that the sharing system in the weir fishery is somewhat complicated. While the individual's share of financial responsibility is usually dictated by his share of ownership, there are deviations. In a number of records obtained, information on such deviations was not provided, since the indebtedness declared referred only to the financial position of the person interviewed, not to the indebtedness of other part owners of the enterprise. In a few isolated cases, field investigators were informed that "the name to whom weir material or equipment was invoiced" served to determine the area of financial responsibility. Still in other instances, it appeared that those who can best afford it are expected to bear the capital expenses.

For these and other similar considerations, no claim can be made here that the capital debt position of the weir fishery is accurately portrayed. Our only evidence is that 33 weir owners declared a capital debt totalling $49,421. For the 86 enterprises just analyzed, the capital indebtedness declared was only $34,622.

FISHING INCOME

The income analysis which follows is restricted to the proceeds accruing to fishermen from weir fishing. Income derived from other fisheries is treated in part in other sections of this report, while supplementary income from other sources, such as from lumbering, farming, etc., is omitted.

One of the best known and commonly adopted methods of measuring an individual's economic activity is to calculate his net income position. This method is here employed. For weir fishermen, it entails two basic steps: (1) the determination of receipts, obtained from the proceeds of the weir catch, and (2) the calculation of weir fishing expenses. The latter in turn entails two measurements: the first, of expenditures, including the maintenance and repair of gear and equipment; the second, of allowances for capital depreciation. Once receipts have been adjusted to cover fishing expenses, the residue is the net disposable share to fishermen before personal taxes.

Receipts. The principal source of receipts for the weir fisherman is the herring fishery. Groundfish, particularly pollock, is also caught in weirs, but is of minor significance relative to herring. Most of the weir-caught pollock is taken in Grand Manan and, although its volume does not bulk large in the total fish landings of the Passamaquoddy region, the income it generates for a number of fishermen is substantial. The main channels of utilization for herring are: (1) canning for human consumption, (2) canning for pet food, (3) fish meal, (4) bait for fishermen, (5) fertilizer and (6) salvage of fish scales for the manufacture of pearl essence.

Data for 86 weir enterprises reveal that total receipts from fish sales were $208,044 in 1956 and $261,632 in 1957. The variations in average receipts by enterprise classes are shown in Table VIII.

TABLE VIII. Average and range of weir receipts by enterprise class, 1956 and 1957.

Enterprises	Weirs	1956 Average	1957 Average
	No.	$	$
72 1-weir	72	2,096	2,318
12 2-weir	24	1,520	2,731
2 3+-weir	10	2,067	2,917

In 1956, 1-weir enterprises averaged the highest, while weirs in the 2-weir enterprise class averaged the lowest receipts. By contrast, 1-weir enterprises had the lowest and weirs in the largest enterprise class the highest average receipts in 1957. However, the spread between the high and low average receipts each year was relatively unchanged. Intra-area variations were more striking as indicated in Table IX.

The year 1957 was a particularly good year for fishermen operating inside the proposed Passamaquoddy power dam sites, especially for those with weir installations along the mainland coast. Average receipts for this particular area were more than four times those of 1956. Even on Campobello Island, inside the proposed dams, receipts in 1957 were more than twice those in 1956. On Deer Island the gains, though modest by comparison, were still in the neighbourhood of 21%.

Such increases in receipts were attributable to greater fish abundance. Our investigations produced no evidence of change or improvement in catching and marketing patterns between 1956 and 1957. Fish supplies in the latter year were disposed of through the same channels of utilization as in the previous year, and prices registered no significant change.

In areas outside the proposed dams the differences in average receipts were much less pronounced and were generally in inverse relation to those in the inside areas. Only weir fishermen on Deer Island experienced higher average gains in 1957 than in the previous year; yet the increase amounted to only about 5%. This was easily nullified by the average receipt decline in other areas, particularly

TABLE IX. Average weir receipts of 86 enterprises, by areas, 1956 and 1957.

	Weirs	Receipts 1956	Receipts 1957
	No.	$	$
(1) Inside proposed power dams			
Mainland	25	785	3,401
Deer Island	3	592	743
Campobello	7	909	2,015
Sub-total	35	794	2,896
(2) Outside proposed power dams			
Mainland	26	2,088	1,610
Deer Island	20	1,950	2,125
Campobello	2	1,973	1,973
Grand Manan	23	3,611	3,128
Sub-total	71	2,539	2,257
(3) Inside and outside dams			
Mainland	51	1,449	2,488
Deer Island	23	1,773	1,945
Campobello	9	1,145	2,005
Grand Manan	23	3,611	3,128
Total	106	1,963	2,468

on the mainland and Grand Manan. The drop in receipts from the sale of fish other than herring, principally pollock, due to scarcity, was responsible for the decline registered in the average weir receipts in Grand Manan.

EXPENDITURES. Total expenditures for the 86 enterprises (106 weirs) here analyzed exhibited but minor variations during the two-year period 1956 and 1957. As shown in Table X, these expenditures were $84,015 in 1956 and $81,435 in 1957—a difference of only 3%. The pattern of expenditure was also relatively invariant, with expenditures for weir material and wages in the neighbourhood of 80% of the total for each of the two years.

TABLE X. Expenditures for 86 enterprises (106 weirs), 1956 and 1957.

Items	1956		1957	
	$	%	$	%
Netting	24,433	29.1	27,139	33.4
Other weir material	31,268	37.3	28,641	35.2
Gas and oil	3,277	3.9	3,248	4.0
Boat repairs	2,574	3.1	2,791	3.4
Wages	12,275	14.6	11,809	14.5
Transportation	2,675	3.2	2,373	2.9
Towing	424	0.5	337	0.4
Interest	1,205	1.4	564	0.6
Other	5,884	6.9	4,533	5.6
Total	84,015	100.0	81,435	100.0

It should perhaps be observed that the expenditures here treated bear little if any relationship to fishing intensity. While total expenditures in 1957, for example, were about 3% below those of 1956, operating income from fishing was 45% higher, despite inflexible prices. The reason, simply stated, is that the principal expenditures associated with weir fishing—weir material, pile driving and the like—must be incurred regardless of the outcome of the catch, good or bad. If a weir is to be operated efficiently, it must not only be built and put in readiness each year, but must be maintained at a reasonable level of potential performance. Thus, the leading determinants of yearly expenditures are: (1) the magnitude of normal repair and maintenance (wear and tear), which varies from one period to another in proportion to the durability of weir components, and (2) the vagaries of the weather, which can inflict heavy, unpredictable tolls.

The analysis by weir enterprise class presented in Table XI reveals variations in most expenditure components. The most striking items by far are netting and other weir material, due largely to the proportion of the total which they

TABLE XI. Average weir expenditures for each enterprise class, 1956 and 1957.

	1-weir enterprises		2-weir enterprises		3+-weir enterprises	
No. of weirs:	72		24		10	
Items	1956	1957	1956	1957	1956	1957
	$	$	$	$	$	$
Netting	248	247	125	227	357	394
Other weir material	286	272	282	203	394	418
Gas and oil	28	28	30	29	55	55
Boat repairs	22	21	9	15	78	91
Wages	137	120	91	114	24	42
Transportation	26	26	23	18	23	9
Towing	6	4	–	–	3	–
Interest	11	6	16	6	–	–
Other[1]	42	16	99	126	45	37
Total	806	740	675	738	979	1,046

[1]Consists mainly of the cost of licenses, telephone calls, postal-box rentals, accounting services and rentals for herring shut-off seines. In the 2-weir enterprise group, the last item is particularly high, one operator alone having paid out $1,871 and $2,557 for rentals in 1956 and 1957 respectively.

represent. For the Passamaquoddy region as a whole, weir material expenditures —netting, rope, brush, stakes and the like—are largely a function of: (a) the weir size, particularly the quantity of wooden material required and the quantity of netting used, and (b) the availability of free material and labour. Price and quality variants are not significant factors in this assessment, due to the localized nature of the market and the use of fairly standard material such as brush, stakes,

etc. Transportation charges also exert a negligible influence on operating cost, in view of the accessibility of materials used.

It can be seen from Table XI that average expenditures on weir material for the 10 weirs in the large-enterprise group were substantially above those for weirs falling in the other two groups. The reasons: weirs in the large enterprise class exceeded the average size for the region, and most of the material including wood was purchased in the market. (The breakdown of weir material in Table XI between netting and other weir material is not accurate. The cost of netting —$357 in 1956 and $394 in 1957—is inflated by the inclusion of expenditures for rope and other miscellaneous items used in 4 weirs for which no breakdown was possible. Also the weirs represented are not typical of those operated in the region. They are owned by two large operators whose method of operation and system of accounts are at some variance with those prevailing in the smaller enterprises.) Weirs in the other two enterprise classes, which exhibited fairly comparable material expenditures, were smaller and composed, at least in part, of owned material acquired and put to use with the help of free labour.

Of the remaining expenditure components in Table XI, three items merit comment. These are: gas and oil, boat repairs and wages.

The variation between enterprise groups in the magnitude of expenditures for both gas and oil and boat repairs shows a pattern analogous to that of weir material expenditures. With respect to gas and oil, average expenditures for a weir in the large enterprise group are approximately twice those for a weir in either the 2-weir or 1-weir enterprises. In the case of boat repairs, expenditures for the same multiple weir group exceed those of other weirs represented by an even higher ratio. The reason, simply enough, stems from the fact that weir operators of the larger business units have more capital items to operate and maintain—in this instance specifically, more boats, scows, cars and other craft or vehicles. This is reflected in Table V which shows average weir investment in fishing capital for the large enterprise group here considered at $8,681, exceeding the overall average of the 106 weirs analyzed by over 30%. By contrast, the average expenditure for wages is outstandingly low for weirs in the large enterprise group. This too is a reflection of capital investment. Except at Grand Manan, wages consist almost exclusively of money paid out to divers and pile driver operators; and of the two costs, that for pile driving is normally greater. Where operators have their own pile driving equipment operated by tendermen, whose reward for all services rendered is a share in the proceeds of the catch, the wage bill is virtually reduced to the outlay required for divers[8]. In consequence, average expenditures for wages for the weirs specified were reduced to only 18% in 1956 and 35% in 1957 of the average wage outlay for weirs in the 1-weir enterprise group.

[8]Pile driving costs are recurrent each year. The need for divers, on the other hand, is largely dependent upon the extent of damage to weir components in a deep water location. Moreover, a number of shallow water weirs can be built and maintained without much assistance from hired divers.

Not unlike investment in weir capital, discussed in the previous section, expenditures revealed appreciable variations between areas in the Passamaquoddy region (Table XII). In the area designated as inside the proposed power dams, average expenditures for each of the years 1956 and 1957 were less than 60% of the regional average. By contrast, weirs situated in the area outside the proposed dams, including Grand Manan, experienced average expenditures which exceeded the regional average by 18–19%.

TABLE XII. Average weir expenditures of 86 enterprises, by areas, 1956 and 1957.

	Weirs	Expenditures 1956	Expenditures 1957
	No.	$	$
(1) Inside proposed power dams			
Mainland	25	490	519
Deer Island	3	399	243
Campobello	7	203	300
Sub-total	35	425	452
(2) Outside proposed power dams			
Mainland	26	731	783
Deer Island	20	462	407
Campobello	2	1,081	1,081[1]
Grand Manan	23	1,685	1,520
Sub-total	71	974	924
(3) Inside and outside dams			
Mainland	51	612	654
Deer Island	23	454	386
Campobello	9	397	473
Grand Manan	23	1,685	1,520
Total	106	793	768

[1]Accurate yearly expenditures could not be obtained for these two weirs. The operators estimated that the same amount was spent each year. The high average of $1,081 reflects the heavy expenditures in one exposed weir ($1,574), which were incurred almost exclusively for stakes and netting.

The lowest average expenditures of any weir group are found on the island of Campobello, inside the proposed power dam site. Here weirs are comparatively sheltered and easy to maintain; and costly pier materials are not required, as on Deer Island, for instance.

At the other extreme is Grand Manan, where the highest weir expenditures prevail. Several factors contribute to the magnitude of these expenditures. One is location. Weirs in this area are concentrated on the east side of the island, where there is little shelter from winds and water turbulence. Damages from weather causes, therefore, are more frequent and costly than in the more protected areas of Passamaquoddy Bay. A second factor is the number of weir

nets used. It is standard practice for a weir operator in Grand Manan to have two sets of nets in use during the regular fishing season, so that the weir is never inoperative even when nets are being cleaned, treated or repaired. Investments in nets, as shown in Table VII, bear out this circumstance and practice. Another important factor is the composition of the "wages" item. In other areas, labour cost consists principally of wages to divers and pile driver operators. On Grand Manan, on the other hand, it includes sizeable disbursements to other recipients —disbursements which, in a number of instances, are the major component of the wage bill. Since diving and pile driving costs are comparable to those prevailing in other areas, average wages, therefore, are singularly high on Grand Manan.

CAPITAL DEPRECIATION. Allowance for capital depreciation was confined to two major items, floating craft (including boats, weir scows, seine racks and pile drivers), and shore equipment. The remaining weir investment items, which consist of nets, poles and other material, have limited durability. Some items, such as brush and stakes, are replaced annually, and only a few materials attain a life span of five years. In all such cases, repairs or replacements were charged to current expenditures.

The rates chosen to calculate depreciation allowances were arbitrarily selected, although they coincided with those employed in other similar primary industry studies. Rates of 7½% and 2½% were applied to floating craft and shore equipment respectively.

The total value of capital equipment declared by 86 weir enterprises amounted to $145,735 in 1956 and $144,866 in 1957. Depreciation allowances for the same years were $4,931 and $4,740.

NET INCOME. Owing to the nature of weir fishing and the prevailing conditions of the market, the availability of fish is the main determinant of the weirman's net income position (Table XIII). In 1957, receipts from fish sales for 106 weirs amounted to $261,632, exceeding the previous year's returns by $53,588. This was due to an increase in fish catches of approximately 6,000 hogsheads, with prices in the various utilization centres remaining substantially

TABLE XIII. Net income of 86 enterprises, 1956 and 1957.

	106 Weirs		Relative	Percentage of receipts	
	1956	1957	change	1956	1957
	$	$	%		
Receipts	208,044	261,632	25.8	–	–
Expenditures	84,015	81,435	–3.1	40.4	31.1
Operating income	124,029	180,179	45.3	59.6	68.9
Depreciation	4,931	4,740	–3.9	2.4	1.8
Net income	119,098	175,457	47.9	57.2	67.1

unchanged[9]. At the same time, expenditures manifested a negative relationship to receipts, so that operating income registered a positive change of 45.3%. The range of this income for 86 weir enterprises was \$-1,671 to \$15,565 in 1956 and \$-1,653 to \$16,117 in 1957. Average net income per enterprise was \$1,385 in 1956 and \$2,040 in 1957; on a per weir basis, it was \$1,123 in 1956 and \$1,655 in 1957.

The distributive shares apportioned to the agents of production also showed considerable variation by areas during the years 1956 and 1957. As can be seen from Table XIV, the average net earnings of labour and capital in the Passamaquoddy region in those two years were both low and subject to quite severe fluctuation. In 1957, which was a good year for weirmen operating within Passamaquoddy Bay, the average operating income per enterprise for that area was still only \$589 to labour and \$406 to capital; in 1956—a comparatively lean year—the returns were \$161 and \$-11 respectively.

TABLE XIV. Distribution of average receipts reported by 86 weir enterprises (106 weirs), 1956 and 1957.

Areas	Receipts		Distributive shares[1] Labour		Distributive shares[1] Capital		Distributive shares[1] Other	
	1956	1957	1956	1957	1956	1957	1956	1957
	\$	\$	\$	\$	\$	\$	\$	\$
Inside proposed dam sites	323	1,179	161	589	-11	406	173	184
Outside proposed dam sites	2,096	1,863	847	774	445	326	804	763
Inside and outside dams	2,419	3,042	1,008	1,363	434	732	977	947

[1]Returns to labour are net cash; returns to capital are net before allowance for depreciation; "other" represents expenditures.

Since the sharing system of wage payment is widely used in the weir fishery—with workers and capital owners both participating in the rewards of risk-taking—it is in some respects analagous to profit-sharing in other industries. In such a situation, it is often difficult to make a precise separation of returns to labour and returns to capital. It can also be somewhat confusing when comparisons are made between firms in the industry which employ different methods of wage payment.

For some purposes, it is useful to consider the net income from fishing without attempting an allocation of shares to the various agents involved. Since one can expect net income per enterprise in any one fishery to vary with the number of men employed in that enterprise, the average net income per man engaged in weir fishing was obtained in Table XV by dividing the average number of men per weir into the average net income per weir. Similarly, since one can

[9]Except for periods of acute demand conditions, such as the war years for instance, this circumstance of "receipt-supply dependence" is historically characteristic of the weir fishery.

expect net income to vary with the amount of capital invested, net income per man per dollar of investment was obtained by dividing net income per man by average capital investment (Table XV).

TABLE XV. Calculation of average net income per weir for 106 weirs (86 enterprises), by areas, 1957.

Averages	Inside proposed dams	Outside proposed dams	Total
Receipts	$2,896	$2,257	$2,468
Expenditures	452	924	768
Operating income	$2,444	$1,333	$1,700
Depreciation	40	47	45
Net income per weir	$2,404	$1,286	$1,655
No. of men engaged per weir	4.40	5.42	5.08
Net income per man	$ 546	$ 237	$ 326
Capital investment	$5,471	$6,250	$5,993
Net income per man per dollar invested	$ 0.10	$ 0.04	$ 0.05

The effect of comparatively high receipts inside the proposed dam sites in 1957, together with relatively constant expenditures, is evident from Table XV. Average net income per man, as well as per dollar invested, including returns to both labour and capital, was more than twice as high inside as outside the proposed dams.

It is interesting to compare the rate of return from capital invested in weirs with that prevailing in other fishing enterprises covered in this study. For Charlotte County as a whole, average net income per man in the weir fishery in 1957 was $326, as compared with an average of $4,536 in purse seining (Table XXI). Reduced to the net income per dollar invested, the comparison becomes $0.05 for weirs and $0.24 for purse seining.

HERRING PURSE SEINERS, 1957

NATURE OF THE FISHERY

A type of purse seining for the removal of fish caught in herring weirs has been known and employed for many years. A fleet of purse seiners, however, is of more recent origin. This type of fishing was first introduced in the Bay of Fundy in the late 1930's. Since then, the fleet has undergone a gradual but uneasy expansion.

The chief characteristic which separates the purse seiner from other forms of herring fishing in the Bay of Fundy is its mobility. The weir is a stationary installation which depends upon the fish coming sufficiently close to shore to be trapped. Purse seiners, however, go in search of fish wherever it may be located in the Bay of Fundy and adjacent waters.

The purse seiner is a highly productive unit, due largely to its mobility and its extended fishing season. In 1957, the total catch of 6 vessels amounted to 21,800,000 lb, or 3,600,000 lb per vessel. As shown in Table XVI, this represented a total value of $201,954, or an average of $33,659 per vessel. There were only 35 men employed on these vessels, an average of 5.8 men per vessel, so that the gross value of landings per man was about $5,700. By contrast, the gross returns from the weir fishery only amounted to about $630 per man in 1957.

TABLE XVI. Receipts from fishing of 6 purse seiners in 1957.

Source	Total	Averages
	$	$
Herring	197,286	32,881
Other species	4,668	778
Total	201,954	33,659

The vessels that constitute the purse seining fleet vary considerably in design. They are of wooden construction and have an average age of 7 years. At the end of 1957, the oldest was 10 and the newest 2 years old. Their range in length was not great, from 48 to 52 feet, and no significant relationship between landings and length was evident. In general, seiners have one feature in common: they are of less sturdy construction and have a lower capital value than other offshore vessels of the Maritimes (Proskie, 1957). This arises from the fact that seiners neither carry fish nor store it on board—their function is restricted to catching operations, since carrying boats are employed to transport fish from the fishing grounds to the processing plants.

The fish caught by purse seiners is sold to both United States and Canadian processing plants. During the winter, the catch is landed at New Brunswick or Nova Scotia plants, since processing plants in Maine, U.S.A., are closed. However, when Maine plants are open during the summer, a large portion of the catch is landed at fertilizer and pet food plants there. Indeed, it is alleged that herring caught by purse seiners is frequently more suitable for pet food or fertilizer than for human consumption. This is especially true when fish are "feedy", that is, having full stomachs. In a weir, fish may be held alive long enough for their stomach contents to be cleared; fish caught in a purse seine, by contrast, soon die and, unless discarded, must be diverted to uses not as exacting in quality as that required of fish intended for human consumption.

The fact that purse seiners dispose of much of their catch at pet food and fertilizer plants undoubtedly accounts for the lower prices which they receive. In 1957, the prices obtained averaged $11.40 per hogshead. By comparison, the average price received for all herring landed in Charlotte County in that year was $14.38 per hogshead. In the latter case, the largest portion of the supplies was obtained from weir fishermen. Of course, what purse seining fishermen lost in price was more than made up by their higher output.

Fishing Effort

During the survey of purse seining, information was obtained on the number of days spent at sea each month. The results of this part of the survey are shown in Table XVII. Since the data only refer to "days at sea", no account is given of all days worked. Most fishermen, however, have considerable work to do on shore, for maintenance of vessels, repair of fishing gear, etc. In one case, it was reported that 60 days were spent on such work.

Table XVII. Fishing effort for 6 purse seiners, 1957.

Month	Total days afloat	Average per vessel
January	119	20
February	117	19
March	118	20
April	50	8
May	5[1]	1[1]
June	58	12
July	101	17
August	103	17
September	95	16
October	65	11
November	31	5
December	17[1]	3[1]

[1]Only one vessel fished.

Apparently, the most intensive fishing effort of seiners in 1957 occurred in the months of January, February and March, with fairly heavy application in July, August and September. Fishing activity was greatly reduced in the months of April, May and June, when purse seiners vacated certain fishing grounds, in deference to weir fishermen, and moved out into the Bay of Fundy.

Capital Investment

While the hull is one of the least expensive capital items of these enterprises, relatively high cost engines are employed (Table XVIII). Heavy engines are required because of the power demands of seining operations and for dependability. Seiners from the Passamaquoddy region (most of them are located on Deer Island and Grand Manan) frequently fish on the Nova Scotia side of the Bay of Fundy, and the heavy, expensive engines are a desirable safety feature.

Electronic equipment constitutes a substantial portion of the capital investment in herring purse seiners—47% of the total investment in boats alone, and 27% of the total investment of the enterprise. There are three main types of electronic equipment used: (1) direction finders and radar, employed as navigational aids, (2) echo sounders and sea scanners, used for locating fish (they also aid in navigation), and (3) radio telephones for communication. The geographic

TABLE XVIII. Average capital investment by items and as a percentage of total investment in 6 herring purse seiners, 1957[1].

Description	Average investment	Percentage of total
	$	
Hull	2,340	12.6
Engine	2,878	15.5
Electronic equipment	4,964	26.7
Other boat equipment	285	1.5
Sub-total	10,467	56.3
Fishing gear	6,796	36.6
Shore installations	1,317	7.1
Total	18,580	100.0

[1]The figures represent estimated current market values.

and climatic features of the area demand navigational aids. The prevalence of fog and the irregularity of the coastline make navigation difficult or impossible without them, except in clear weather. Herring may be plentiful in the Bay of Fundy, but it is an elusive fish, and electronic aids are considered more dependable for locating a catch than other means of detection. They are considered an essential adjunct to modern herring seining operations.

Fishing equipment constitutes about 40% of the total invested capital in these seiners, the largest single item. In addition to purse seines, which averaged $4,446 per vessel in 1957, three of the enterprises studied owned herring shut-off seines. These ranged in value from $2,600 to $7,000 per vessel making, therefore, an average total investment in fishing gear per enterprise of $6,796.

Five of the enterprises covered owned shore equipment. These installations were used chiefly for the storage of fishing gear during the off-season. Their average value per enterprise was $1,317, which gave an average total investment per enterprise in all equipment of $18,580.

FISHING INCOME

As pointed out earlier, the number of purse seining enterprises covered in this study was small and confined to the fishing operations of only one year. For this reason, only a limited analysis of fishing income was undertaken omitting, therefore, any reference to many of the relationships which are usually drawn in studies of this type between individual expenditures and total expenditures, and between expenditures and receipts.

Average expenditures, as shown in Table XIX, amounted to $6,396 in 1957, or approximately 20% of the gross value of landings. The range of costs was very wide, with the vessels having the greatest landings also incurring the highest costs. The largest single cost item was that associated with the repair of catching gear. This is not surprising, since catching gear forms the greatest single component of invested capital and is an item which is subject to considerable wear

TABLE XIX. Average expenditures in dollars and as a percentage of total expenditures for 6 purse seiners, 1957.

	Average	Percentage of total
	$	
Maintenance and repair		
Hull	384	6.0
Engine	691	10.8
Catching gear	2,639	41.3
Electronic equipment	275	4.3
Sub-total	3,988	62.4
Other operating expenditures		
Fuel, oil and grease	1,184	18.5
Food	1,060	16.6
Marine insurance	27	0.4
Miscellaneous	137	2.1
Sub-total	2,408	37.6
Total	6,396	100.0

and tear. Two other major items of cost were (a) fuel, oil and grease, and (b) food. Together, these three items constituted 76% of all expenditures.

The purse seining enterprises of Passamaquoddy Bay, like those in most deep sea fisheries, are co-adventurous, since the earnings of crew members are dependent upon the gross value of the catch, the cost of producing it and the portion allocated to owners of the capital. It is common practice to apportion a share of total receipts to the boat and, in some cases, to allow a share for the fishing gear. Combined, this is called the capital share, and varied in the sample from 20 to 33⅓% of total receipts. The balance forms the gross crew share, from which the crew's operating expenditures (food and fuel) are deducted. Then what remains—the net crew share—is distributed to the men in the crew, including the captain, on an equal basis. The capital share bears all other expenses.

The actual earnings of capital of the 6 purse seiners studied are shown in Table XX as $4,172 per vessel, after allowing for depreciation. Relative to invested capital, this represented a return of 22.4%. The amounts charged for depreciation were: 7½% of the value of vessels fully equipped and 2½% of the value of shore installations. Normally, fishermen charge depreciation on fishing

TABLE XX. Distribution to labour and capital of average operating income and ratio to total receipts, 1957.

	Average per vessel	Percentage of total receipts
	$	
Operating income	27,263	80.9
Net crew share	22,273	66.1
Net capital share	4,990	14.8
Depreciation	818	2.4
Net earnings of capital	4,172	12.4

equipment to the full amount allowed by the regulations governing income tax, which may or may not bear much relationship to the useful life of the asset. In studies of this kind, a deduction of 7½% is usually made for the depreciation of fishing vessels.

The 6 purse seining enterprises paid $133,636 to 35 crew men in 1957. This amounted to $22,273 per enterprise, or $3,818 per man. There was a considerable range in income, with 1 vessel having earnings of only $529 per man, and an actual loss in the capital account.

For some purposes, it is more meaningful to analyse the net income position of an enterprise before the allocation of shares to capital and labour. Table XXI has been prepared to permit a comparison of the return arising out of capital

TABLE XXI. Average net income as related to capital and labour employed for 6 purse seiners, 1957.

Average	$
Receipts	33,659
Expenditures	6,396
Operating income	27,263
Depreciation	818
Net income per enterprise	26,445
Net income per man	4,536
Net income per man per dollar invested	0.24

investment in purse seiners with that of other fishing enterprises in this general study. The net income of capital and labour so derived amounted to $26,446 per enterprise, or $4,536 per man. Reduced to the net income per dollar invested, the result was $0.24. This compares favourably with rates in other fishing enterprises of the Passamaquoddy region, viz., $0.05 for weirs and $0.33 for herring carriers.

Notwithstanding the favourable results shown in this analysis, there are market, social and institutional restrictions which impose limits upon the scope of purse seining activity in the Bay of Fundy. Not only do existing channels of utilization place limitations upon the size of the fresh herring market, but processing plants often restrict their purchases, by preference, to supplies from weir fishermen. Moreover, local pressure against purse seining, particularly on the part of weir interests and lobster fishermen, has resulted in restricting the movements of seiners to certain distances from shore and from the site of stationary fishing gear.

During the course of our survey, 2 of the 18 seiners licensed in 1957 did not operate because the market would not absorb their catch. It was further recognized, as demonstrated in Table XVII, that the fishing intensity of the operating seiners was restricted during the spring and summer months, when weir catches were at their peak. Thus, the attractiveness of purse seining as a

field of investment is seriously impaired, since the optimum returns of an unfettered and efficiently managed fleet are neither known nor, under present conditions, obtainable.

THE HERRING CARRIER FLEET, 1956 AND 1957

Nature of Herring Carrier Trade

A herring carrier service was first introduced in the Bay of Fundy to meet the needs of the weir fishery. Due to the decentralized nature of weir fishing—the dispersion of weir sites and the multiplicity of owners—and the centralized nature of herring processing, individual weir owners found it impractical to carry their own fish to market. Indeed, the maintenance and operation of a vessel of sufficient size and seaworthiness, to carry fish over the distances involved, would have imposed fixed costs which the individual weir enterprise would have found difficult to meet.

The service provided by herring carriers today is not confined to the weir fishery. It has been extended to purse seiners, beginning in the 1930's. In this more recent role, carriers enable seiners to specialize in the location and capture of fish, without costly interruption for delivering the catch to market. In this way highly capitalized equipment, such as the seining method of fishing employs, can be used most effectively.

The existing fleet of carriers consists of vessels operated (a) by herring processing plants and (b) by private individuals. The former was excluded from the survey upon which this report is based. The latter are primarily engaged in transporting herring to processing plants situated in the United States. Domestic herring processors in Charlotte County maintain their own carrier service, and only infrequently obtain processing supplies from the privately operated or independent[10] carriers.

The operations of all carriers are, of course, not confined to the herring trade. This is particularly true of carriers stationed on Deer Island and Grand Manan (Table XXII). Of the 46 vessels included in the sample survey, about half carried fish other than herring. Indeed, if receipts can be taken as a guide, the carrying of herring was a subsidiary operation for 11 vessels in 1956 and for 12 of them in 1957. The break-down of receipts by species transported was not available in all cases, but it seems likely that lobsters and fresh pollock contributed significantly to carrier income. Herring scales, scallops and smoked and salted fish are also transported, but the survey indications are that the quantities involved are small.

There is considerable variation in the price paid to carriers for the transportation of herring. The main determining factor appears to be the distance travelled. Some carriers travel long distances to pick up their cargo—to points

[10]"Independent", in this context, means that operators of carriers are free to dispose of their cargo to buyers of their choice. In fact, however, many privately operated carriers deliver fish under contract to specific plants; and contractual arrangements differ within the industry.

TABLE XXII. Receipts from herring as a percentage of total receipts for 46 herring carriers, by areas, 1956 and 1957.

	Deer Island	Campobello Island	Grand Manan	Total
	%	%	%	%
1956				
Herring	75	93	63	68
Other species	25	7	37	32
Total	100	100	100	100
1957				
Herring	64	91	68	72
Other species	36	9	32	28
Total	100	100	100	100

on the coasts of Nova Scotia or Maine—while others limit their movements between points situated within relatively sheltered waters, in and around Passamaquoddy Bay. During the survey, the prices encountered ranged from $2 to $8 per hogshead.

As might be expected, the larger carrying vessels tend to travel longer distances and, in turn, receive higher prices than the smaller boats (Table XXIII). They also tend to rely more on purse seiners than on weirs for their supplies.

TABLE XXIII. Average price received per hogshead for 31 herring carrier enterprises, by size of boat, 1956 and 1957.

Size of boat	Average price per hogshead	
	1956	1957
	$	$
11–16 gross tons	3.90	3.18
17–22 gross tons	3.60	3.26
23–28 gross tons	3.61	4.28
29 or more gross tons	5.68	5.26
Total	4.36	4.08

In fact, their main function is to provide a service to vessels fishing in unsheltered waters, where small carriers cannot venture for lack of seaworthiness. Moreover, when purse seiners make a catch they must dispose of it, since they are not equipped either to hold or store fish at sea for any length of time. The smaller carriers cannot hope to cater to these demands. On the other hand, they are well suited to the demands of the weir fishery, since weirs are always close to shore and the fish which they trap can be held for indefinite periods when the need arises.

Information on receipts, expenditures and capital investment for 46 enterprises was recorded in detail during the survey. The vessels ranged in size from 11 to 43 gross tons, averaging 22 gross tons. Their average length was 53 feet, with a range of 41 to 66 feet. Differences in size were exhibited between the major areas of the region, as indicated in Table XXIV.

TABLE XXIV. Average boat size for 46 herring carrier enterprises, by areas, 1957.

Averages	Deer Island	Campobello Island	Grand Manan	Total
Gross tonnage	18.4	21.1	23.8	21.8
Length in feet	50.5	53.3	54.3	53.1

In construction, the carriers are wooden, with wooden tanks installed in the middle of the hold. The more modern vessels are powered with diesel engines and are equipped with the latest electronic aids such as radio telephone, loran, depth sounders, etc. The average age of these vessels was 14 years in 1957, although some were very old and others relatively new. One vessel of unusual durability was included in the sample, it being 41 years old in 1957.

"CARRYING" EFFORT

Information on the seasonal nature of herring carrying activities was collected during the survey from some of the enterprises. Since the pattern in 1957 was not much different from that of 1956, and since a larger number of observations was available for the earlier year, the data in Table XXV are restricted to 1956.

TABLE XXV. Monthly as a percentage of total receipts for carrying herring, 23 enterprises, 1956.

Month	Deer Island	Campobello Island	Grand Manan	Total
	%	%	%	%
January	...	...	3	2
February	...	...	2	2
March	...	...	...	...
April	5	...	...	...
May	...	...	1	1
June	4	10	11	10
July	20	39	21	23
August	29	22	23	23
September	25	18	22	22
October	13	7	10	10
November	3	4	5	5
December	1	...	2	2
Total	100	100	100	100
No. of observations	6	3	14	23

It must be emphasized that the percentages above apply only to herring carrying. Many of the boats transport other species of fish, particularly lobsters, in the early summer and early winter. It will be noted that most of the work in 1956 was done during 4 months on Deer Island and during 5 months in the other two areas. The peak month was July on Campobello Island, August on Deer Island and Grand Manan. Only one carrier (on Grand Manan) worked in January and February, and none worked in March.

Considerable risk is involved in operating a herring carrier with a 1-man crew particularly on the longer voyages in unsheltered waters. Only 5 of the 46 skippers interviewed said that they normally worked alone. In all probability, these did not often make long trips. Their vessels were relatively small—in the 15 to 18 gross ton range—and 4 of the 5 were located on Deer Island. Two enterprises, both on Grand Manan, normally employ a 3-man crew. Both of these vessels are over 27 gross tons.

Capital Investment

The magnitude of capital investment in the average herring carrier bears a close relation to that in a typical weir. In 1957, for instance, average investments were $6,496 for a carrier and $6,000 for a weir. Moreover, the differences in average investment per carrier among the major areas of the region are also quite striking, as they are in weir investment.

As is obvious from Table XXVI, average investment in carriers on Deer Island in 1957 was low relative to that in other areas of the region. There are two

Table XXVI. Average capital investment per enterprise in 46 herring carrier enterprises, by types of equipment and by areas, 1957.

Type of equipment	Deer Island		Campobello Island		Grand Manan		Total	
	$	%	$	%	$	%	$	%
Hull	1,902	67	3,478	49	4,206	52	3,445	53
Engine	742	26	2,150	30	2,311	28	1,843	28
Other[1]	194	7	1,504	21	1,636	20	1,208	19
Total	2,838	100	7,132	100	8,153	100	6,496	100

[1]Mainly navigational aids.

outstanding reasons: the size of the vessels and their age. In the case of size, only 1 out of 13 vessels from Deer Island was more than 23 gross tons, whereas 2 out of 7 and 13 out of 26 from Campobello and Grand Manan respectively were in this larger size category. As to age, the average for Deer Island vessels was 17 years, as opposed to 12 years in each of the other two areas.

The investment category which exhibits the greatest difference between Deer Island and the other areas is that classified as "other" in Table XXVI. This item is composed mainly of aids to navigation. Since the operations of Deer Island carriers are largely confined to the trade arising from the weir fishery in

and about the sheltered waters of Passamaquoddy Bay—as opposed to the movements of the larger vessels of other ares—the need for expensive navigational aids does not, of course, arise.

"Carrying" Income

Receipts. The total receipts of herring carriers displayed very little change during the years 1956 and 1957. However, there were wider variations by areas within the region, as indicated by the average enterprise receipts in Table XXVII.

It can be seen that average gross receipts per enterprise were higher on Deer and Campobello Islands and lower on Grand Manan in 1957 than in 1956.

Table XXVII. Average receipts per enterprise and percentage change for 46 herring carriers, by areas, 1956 and 1957.

Year	Deer Island	Campobello Island	Grand Manan	Total
1956	$1,904	$6,307	$8,636	$6,379
1957	2,352	6,657	8,289	6,363
Percentage increase	24%	6%	–	–
Percentage decrease	–	–	4%	–

Actually, increases were common for Deer Island vessels, with 11 out of 13 reporting additions to receipts in 1957. On Grand Manan, on the other hand, the decreases were largely accounted for by 3 of the 26 carriers included in the survey of that area.

It has been mentioned earlier in this report that 1957 was a comparatively good year for the weir fishermen of Passamaquoddy Bay. It was to be expected, therefore, that the herring carriers of Deer and Campobello Islands, but more particularly of Deer Island, would benefit from this improved catch by reason of their location and accessibility.

Expenditures. The two major items of expenditure associated with the operation of a herring carrier are (a) maintenance and repairs and (b) fuel. As shown in Tables XXVIII and XXIX, average wages paid in either 1956 or 1957 did not exceed 6% of receipts in any area, while the average of "other" expenditures only reached a maximum of 4% in either of the two years.

For the region as a whole, average expenditures per enterprise showed little change during the 2 years studied—$2,296 in 1956 and $2,209 in 1957. There was a slight variation in the magnitude of the expenditure components in the 2 years, but each of the main categories remained almost constant in relationship to receipts.

Considering the three areas separately, average expenditures in Grand Manan were about the same in both years, on Campobello Island the most outstanding

TABLE XXVIII. Average expenditures in dollars and as a percentage of receipts for 46 herring carriers, by items and by areas, 1956.

Item	Deer Island		Campobello Island		Grand Manan		Total	
	$	%	$	%	$	%	$	%
Maintenance and repairs	281	15	1,042	16	1,321	15	984	15
Fuel	225	12	936	15	1,074	12	813	13
Wages	0	...	356	6	452	5	310	5
Other expenditures[1]	6	...	131	2	296	4	189	3
Total	511	27	2,465	39	3,143	36	2,296	36

[1]Includes food, boat insurance, car expenses, radio licenses, anchorage fees, customs dues and sick mariners' insurance in order of decreasing importance. All amounts are rounded.

TABLE XXIX. Average expenditures in dollars and as a percentage of receipts for 46 herring carriers, by items and by areas, 1957.

Item	Deer Island		Campobello Island		Grand Manan		Total	
	$	%	$	%	$	%	$	%
Maintenance and repairs	259	11	989	15	1,312	16	965	15
Fuel	309	13	712	11	970	12	744	12
Wages	26	1	429	6	377	4	286	5
Other expenditures[1]	38	2	202	3	305	4	214	3
Total	632	27	2,332	35	2,964	36	2,209	35

[1]Includes food, boat insurance, car expenses, radio licenses, anchorage fees, customs dues and sick mariners' insurance in order of decreasing importance. All amounts are rounded.

change was the drop in fuel costs in 1957, while on Deer Island a significant increase was registered in average fuel, wages and "other" expenditures in 1957.

The differences among these major areas were more pronounced in 1956 than in 1957. Still, in each year, the main differences were in wages and "other" expenditures. Generally speaking, these are due to variations in vessel size. The larger the vessel, the larger the crew and the larger the proportion of total expenditures for wages and "other" expenditures. For the smaller vessel class, these costs are often negligible, since the owner often operates the carrier without help, has little or no wages to pay and is spared much of the "other" expenditures such as food, insurance and the like. This was particularly true in 1956 with respect to Deer Island vessels. In 1957, which was a good fishing year for weirmen in Passamaquoddy Bay and, by the same token, a busy year for Deer Island carriers, more money was spent on these particular items; yet, it still represented a small portion of total expenditures, and fell far short of the outlay for wages and "other" expenditures in the two other areas of the region.

It is interesting to compare average expenditures and average receipts for the various vessels by size classes. These are expressed in percentages in Table XXX.

The change in the cost of maintenance and repairs is the main cause of the differences between 1956 and 1957. For vessels in the 11–16 gross ton category, this cost item fell by 4% of receipts; for those in the 23–28 range, it increased by 5%; and for the largest vessel group, it fell by 3%. No change was experienced by the vessels in the 17–22 gross ton class.

TABLE XXX. Average expenditures as a percentage of receipts for 46 herring carriers, by items and by size classes, 1956 and 1957.

Item	11–16 gross tons		17–22 gross tons		23–28 gross tons		29 or more gross tons	
	1956	1957	1956	1957	1956	1957	1956	1957
	%	%	%	%	%	%	%	%
Maintenance and repairs	20	16	14	14	11	16	18	15
Fuel	13	12	11	11	15	14	11	10
Wages	2	4	4	4	7	8	5	3
Other expenditures	3	4	3	3	3	4	4	3
Total	38	36	32	32	36	42	38	31

The repair of equipment is a variable expenditure item. Breakdowns are unpredictable, and often the outcome of "ill luck"; but when they occur, repair must be effected regardless of cost if the enterprise is to be kept in operation. Again, in other cases, "repairing" means rebuilding and, since rebuilding often takes place during the slack season, the receipts from fishing operations may not be greatly affected. Often, however, the cost of rebuilding is charged off in one year, so that the percentage of receipts required to meet expenditures in that particular year can be quite high.

Changes in wages from year to year and from one vessel class to another are perhaps not too significant, in view of the influence of institutional arrangements (payment on a time rather than on a share basis appears more prevalent in the case of vessels in the larger size groups).

NET INCOME. Wages must be deducted and depreciation charges added to the expenditure data before the average net income per carrier enterprise can be calculated. Since, by previous reference, some major alterations (capital investments) are apt to be charged off as repair expenditures, a straight-line depreciation rate of 5%, rather than the usual 7½%, was used in determining net income.

The trends in Table XXXI result from factors which have already been discussed in earlier sections of this report. The changes between 1956 and 1957 in net income per man per dollar of capital investment are of particular interest[11].

[11]The methods employed to arrive at net income per man are explained in connection with Table XV.

TABLE XXXI. Calculation of average net income for 46 herring carriers, by areas, 1956 and 1957.

Average	Deer Island	Campobello Island	Grand Manan	Total
	$	$	$	$
1956				
Receipts	1,904	6,307	8,636	6,379
Expenditures[1]	511	2,109	2,691	1,986
Operating income	1,393	4,198	5,945	4,393
Depreciation	156	376	389	321
Net income per enterprise	1,237	3,822	5,556	4,072
Net income per man	732	2,055	2,724	2,132
Net income per man per dollar invested	0.23	0.27	0.35	0.33
1957				
Receipts	2,352	6,657	8,289	6,363
Expenditures[1]	606	1,903	2,587	1,923
Operating income	1,746	4,754	5,702	4,440
Depreciation	142	357	408	325
Net income per enterprise	1,604	4,397	5,294	4,115
Net income per man	949	2,199	2,595	2,132
Net income per man per dollar invested	0.33	0.31	0.32	0.33

[1]Less wages.

On Deer Island, an increase of 24% in receipts (Table XXVII), together with a decrease in maintenance and repair costs which more than offset added expenditures in other categories (Tables XXVIII and XXIX) and a decline of $300 in the amount of capital invested, resulted in a much higher net income per man per dollar of capital investment in 1957 than in the previous year. This ratio increased to a lesser extent on Campobello Island. Here receipts played a minor role, since they increased by only 6%, while expenditures declined, mainly in fuel, by 4% of receipts.

On Grand Manan, net income was lower in 1957 than in 1956. Since expenditures as well as receipts declined, the $129 decrease in net income per man must be attributed mainly to the decline in the volume of business. In addition, several capital purchases were made on Grand Manan in 1957, and average capital investment was higher that year. This increase, without any compensating increase in the average net income of the enterprise, resulted in reducing the net income per man per dollar invested by almost 10%.

The results for both 1956 and 1957 indicate that the larger herring carriers included in this study experienced diminishing returns to capital. Data providing three measures of net income by vessel size classes are presented in Table XXXII.

The main reasons for the changes between 1956 and 1957 are fairly apparent. For the smallest vessels, there was a 7% increase in receipts and a 2% decrease in the proportion of receipts required to pay for expenditures. It seems probable

TABLE XXXII. Calculation of average net income for 46 herring carriers, by vessel sizes, 1956 and 1957.

Average	11–16 tons	17–22 tons	23–28 tons	29 or more tons
	$	$	$	$
1956				
Receipts	3,300	4,318	11,034	11,235
Expenditures[1]	1,193	1,211	3,246	3,667
Operating income	2,107	3,107	7,788	7,568
Depreciation	156	264	344	703
Net income per enterprise	1,951	2,843	7,444	6,865
Net income per man	1,141	1,520	3,511	3,238
Net income per man per dollar invested	0.36	0.29	0.51	0.23
1957				
Receipts	3,546	4,702	9,136	11,842
Expenditures[1]	1,130	1,299	3,104	3,375
Operating income	2,416	3,403	6,032	8,467
Depreciation	147	249	357	755
Net income per enterprise	2,269	3,154	5,675	7,712
Net income per man	1,268	1,687	2,677	3,638
Net income per man per dollar invested	0.43	0.34	0.38	0.24

[1]Less wages.

that maintenance and repair costs were abnormally high in 1956. These trends, combined with the usual depreciation charges and very few capital purchases, led to much higher net income per man per dollar invested in 1957.

The story was much the same for vessels weighing between 17 and 22 gross tons, except that in this case expenditures remained steady. Net income per man per dollar invested in 23–28 ton vessels, which was very high in 1956, fell to 38 cents in 1957. Receipts declined by 17%, while the cost of maintenance and repairs, expressed as a percentage of these receipts, increased by 5%. In addition, capital purchases were made by owners of vessels in this size class, so that average capital investment was higher in 1957 than in 1956.

For the largest vessels, slightly higher receipts and considerably lower expenditures again, particularly in maintenance and repairs, resulted in a large increase in net income per man. Average investment per vessel rose by $1,000 between 1956 and 1957, so that the net income per man per dollar of capital investment showed only a slight increase.

It must be stressed, however, that returns to capital and to labour do not depend entirely upon the size of the enterprise or the outlay in capital. As was mentioned earlier in this report, there are certain rigidities in the herring fishery; and these can work to the advantage of some herring carrier operators and against others. Moreover, managerial skill always plays an important role in the measure of success which any enterprise attains. In the carrying trade, this has particular application in the development of personal contacts in the promotion of business

with plant operators and fishermen, in keeping the assets employed most effectively throughout the fishing year, in the choice of the most economically efficient gear and equipment, in the proper care and maintenance of assets and in other relevant business matters.

SUMMARY AND CONCLUSIONS

General

The economy of Charlotte County is highly dependent upon the resources of the sea. Allowing for considerable movement of workers among primary fishing, agricultural and forestry activities, there were approximately 1,350 men engaged in fishing operations in 1957, with upwards of 1,300 who were predominantly women employed seasonally in fish processing plants. This represented over one-third of the labour force in the County, as of 1955, the last year for which figures were available (Grasberg and Whalen, 1958). Gross annual returns to fishermen, as measured by the landed value of fish averaged $1,900,000 during the period 1948–1957; and it is estimated that the total net income to persons engaged in the fishing industry was about $3,000,000 in 1957. This would include the net income of fishermen, of persons engaged in the fish-carrying trade and of persons employed in fish processing plants.

As is true of fishing areas elsewhere on the Canadian east coast, the primary fishing industry of Charlotte County is not highly capitalized. In 1957, private fishing capital—boats, gear and shore equipment—amounted to $4,100,000 or an average of about $3,000 per fisherman. By contrast, the secondary division of the industry is, for the most part, concentrated and large-scale. It maintains a capital stock which, in 1957 was estimated at about $7,500,000. The total private investment in the fishing industry, therefore, is estimated to be in the vicinity of $11,600,000.

Herring is the leading fishery resource of the area. The erratic behaviour of this species is established historically by the wide variations in catches from year to year. For the 10-year period ending with 1957, the yearly value of landings to fishermen in Charlotte County averaged $1,000,000. The method of capture is still principally by means of weir installations, although purse seiners have been in use since the late 1930's and have proven quite effective and efficient in the Bay of Fundy. The herring fishery also maintains a carrier fleet, which is adjunctive to both weir fishing and purse seining. Altogether, in these three sectors of the primary herring fishery, there is a capital investment of about $2,000,000.

The weir fishery, like most inshore fisheries, is decentralized and dependent upon an intensive application of labour. It is organized in small enterprise units, consisting typically of one weir (about 4 men per weir), in which the traditional "lay system" of payment to labour and capital still prevails. About 50% of the weir workers are hired labourers—tendermen, so-called—who have no equity in the capital of the enterprise but who tend and operate weirs for a predetermined

share of the season's catch. Only in a few isolated cases do they receive a stipulated money wage. Due to this circumstance, capital owners are relieved of a great deal of the risk and uncertainty associated with fishing—risks which are further reduced by the fact that equity capital in most weir enterprises is small and spread among several owners.

Despite a basic similarity in weir installations in Charlotte County, considerable variation in weir investment exists within and among the different parts of the region. This is due to differences in weir size and in the topographic and oceanographic environment. Survey data obtained for the years 1956 and 1957 revealed an average investment in weirs, including associated weir gear, of about $5,500 inside Passamaquoddy Bay and of about $6,200 outside the Bay. Total investment in weir enterprises for the entire region was placed at $1,700,000. Approximately 1,100 men are engaged in the weir fishery.

The income derived from the weir fishery is largely a function of the success of the catch. Owing to the nature of the market, the prices which fishermen receive are relatively inflexible. At the same time, operating expenditures are fairly rigid and subject to little influence from variations in receipts. In consequence, fluctuations in catches within the region and from year to year can engender wide variations in earnings among fishermen; and a series of unsuccessful catches can leave the weirman in rather poor circumstances.

Data obtained on 86 weir enterprises for the years 1956 and 1957 provide some evidence in this connection. In 1957, the operating income of these enterprises ranged from $-1,653 to $16,117; in 1956, from $-1,671 to $15,565. The average net income per enterprise was $2,040 and $1,385 respectively, for the same two years; and the average share to capital, before allowance was made for depreciation, was only $732 and $434. Despite such low and often discouraging returns, weir fishermen, as a class, continue to maintain their investment in this operation and are generally opposed to the application of alternative methods of fishing herring.

This situation is unlikely to endure. The weir fishery is marginal and, as such, is becoming less and less capable of adjusting to the conditions of a growing economy, particularly rising costs and improving standards of living. Its displacement by fisheries of a more mobile and productive character seems an eventual certainty.

In contrast with the stationary weir, the purse seiner is a mobile, highly capitalized fishing enterprise. The fleet at present is composed of seventeen vessels, with 4–7 men per vessel, representing a capital investment of about $170,000.

While seiners operate under high fixed costs, their catching performance permits the recovery of fairly high returns. Data on 6 seiners covering 1957 operations revealed an average net income per vessel of $26,445. Average crew earnings were $3,818 per man, while the net boat share averaged $4,172. A return of 22.4% on total invested capital is thus indicated.

Notwithstanding this favourable performance, the history of the seining fleet has been one of uneasy expansion. Even today, the scope of its operation is seriously restricted. This arises from the limited market for fresh herring and the local opposition to seining activity, particularly on the part of weir interests and lobster fishermen. As a result, seiners operate much like a fettered fleet: their movements are restricted to certain distances from shore and from the site of stationary fishing gear; and their fishing effort must often be reduced, due to the inability of the market to absorb the catch.

Under existing conditions of demand for fresh herring, the prospects for increased purse seining operations in the Bay of Fundy are not encouraging. This could be a short-run condition. In the long run, there is hope that new channels of herring utilization will emerge to alter the existing demand–supply relationship and, thereby, serve to reduce the local opposition to the application of efficient capital in the herring fishing industry.

The herring carrier fleet is a necessary adjunct to the weir and purse seining fisheries. The vessels vary greatly in size—from about 40 feet to 65 feet—and carry crews of 1–3 men. In 1957, there were 57 independently operated vessels engaged in the carrying trade. Survey data covering 46 of these vessels show they represent an average capital investment of \$6,496. Values ranged from \$350 to \$21,650, due to size differences and age composition.

The total net income from carrying operations—derived mainly from the herring trade—showed little change during the 2-year study. The average per vessel was \$4,072 in 1956 and \$4,115 in 1957. This was due on the one hand to the demand–supply relationship for the commodity transported and, on the other hand, to the absence of fluctuations in both receipts and expenditures in the region as a whole.

The Effects on the Primary Herring Fishery of the Construction of Power Dams in Passamaquoddy Bay

This assessment is confined to two major considerations. The first is the direct physical damage arising from the installation of hydro-electric power dams. The second is the indirect effect of changes in fish abundance and environmental conditions relating to the present status of the fishing industry. It is based upon the results of oceanographic and biological studies that were made available for the preparation of this report.

1. Direct physical damages

According to present knowledge, 6 weirs are situated sufficiently near the power dam sites to be destroyed by the proposed project. The replacement value of weirs including all associated gear inside the site of the proposed dams has been calculated to average \$5,500. Assuming, therefore, that weir values in the vicinity of the dam sites do not differ from the area average, the total replacement value to be considered would amount to \$33,000.

It should be emphasized that the area was not surveyed for purposes of this appraisal. The cost figures were derived from a sample study of the weir fishery

of Charlotte County and are, therefore, provisional. The area where the dams are to be installed and the immediate vicinity where weir sites exist would have to be surveyed by a competent party before conclusive estimates of the cost of damages to weir installations could be prepared.

2. Indirect effects

Fisheries biologists predict no change in herring abundance in the Passamaquoddy region following the completion of the proposed power project. In consequence, the operations of herring purse seiners and herring carriers should not be disturbed. However, a number of environmental changes are expected to affect the efficiency of weir installations in the area. They are assessed under the following headings:

(i) Water levels. On the basis of predicted oceanographic changes in Passamaquoddy Bay, weirs in this area will not be operated at their present locations unless they are modified and altered in size to fish approximately 10 additional feet of water. In particular, weir stakes and nets will need to be larger to suit the new water levels. The average value of weirs including seines in the area is about $4,600, and the cost of weir construction can be expected to rise approximately $1,000 after the dams are installed. In addition, the average costs of annual maintenance and repair could increase by about $100 per weir.

There were 69 weirs operated in the high pool in 1957, with 11 additional licensed weir sites which were not operated in that year. The initial increase in weir construction cost in this area, therefore, could be expected to range from $69,000 to $80,000. The increase in total annual operating costs could range from $6,900 to $8,000.

Admittedly, some weir owners would have the alternative of relocating their weirs closer to shore or at sites farther distant. However, in a number of instances this might not be feasible, owing to the topography of the immediate environment or the lack of suitable sites elsewhere. In any event, it should be recognized that a certain element of disruption and, indeed, of cost—either for material or for labour—would be experienced by the majority of weir owners in the area designated as the high pool.

It is not expected that the degree of disruption to weir fishermen in Cobscook Bay would be as serious. In the first place, there are only 12 weir sites. Secondly, predicted oceanographic changes indicate, in a general way, the reverse of the water level conditions forecast for Passamaquoddy Bay. Weirs, therefore, could be fished at their present sites, although fishing in approximately 5 feet less water.

If fishermen chose to leave their weirs in their present locations in Cobscook Bay, the size of weir gear could be reduced to adjust to the new water levels. This would decrease construction and operating costs, although it might also result in a reduction of weir efficiency. On the other hand, if fishermen wished to employ existing gear to maximum potential efficiency, they would have to relocate their weirs, if alternative, suitable sites were to be found. Additional costs would largely be confined to labour in the first year of construction, and should not be too significant.

(ii) WOOD BORERS. On the basis of predicted changes in water temperatures following the construction of dams, wood borer activity is expected to increase. While it is impossible at this stage to measure the extent of damage likely to result from this source, it should be recognized that the durability of wooden structures within the bays will be diminished. Thus, the life of weir stakes, poles and other wooden weir components will be reduced, which will add to annual operating costs.

(iii) ICE FORMATION. The temperature changes which are forecast lead to the conclusion that the shoreward fringes of Passamaquoddy Bay (except at and near the dams) will have ice cover during the winter months after the dams are installed. In this event, weir fishermen will be faced with two choices: either to dismantle all structural weir material before the onset of winter, for rebuilding in the spring; or to leave the structures to the hazards of winter and to replace them each spring if necessary. Whatever course is followed will add to existing weir operating costs.

(iv) TIDAL SCOUR. The construction of the dams will result in some reduction of tidal currents and wave actions, both of which now cause some damage to weirs. To some extent, this will reduce the increased costs arising from other environmental changes.

The conclusion emerging from the interaction of the changes described is that average weir expenditures are likely to rise appreciably inside Passamaquoddy Bay after the installation of the proposed dams. In view of the nature of the prevailing weir fishery—high, relatively inflexible costs, with correspondingly low returns—it is conceivable that weir owners would not long continue to maintain their investment in weirs in this area. Should this happen, a capital investment of about $440,000 could eventually be displaced.

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LIST OF TABLES

Actions and Interactions of Temperature, Light Intensity and Nutrient Concentration on the Growth of the Green Alga, *Chlamydomonas reinhardi* Dangeard[1,2]

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ABSTRACT

The unicellular green alga, *Chlamydomonas reinhardi*, was cultured at several temperatures in Chu's No. 10 medium under 150 foot-candles illumination. Specific growth rates based on cell counts were found to fit a typical activity curve. The range of temperature tolerance was 6°C to 35°C and the optimum was 28°.

The culture series was repeated at light intensities of 75, 110 and 200 f-c in turn. These changes in illumination did not alter the limits of temperature tolerance or the optimum, though the reduced intensities caused decreases in growth rates. At the reduced intensities light acted as the typical limiting factor. At 200 f-c the growth temperature relation was the same as that for 150 f-c, indicating that some factor other than light intensity had become limiting at the latter levels.

The series was then repeated with the light intensity held at 200 f-c but with the total concentration of nutrient salts doubled. This accelerated growth between 12° and 30°, showing that some nutrient salt was indeed the limiting factor in the experiments with 200 f-c. However, the increase in salt concentration also shifted the lower limit of temperature tolerance up to 12° and moved the optimum down to 18°. Hence the salt concentration must have played some role besides that of limiting factor.

Finally, the results of this investigation are discussed from the standpoint of the system of environmental factors described by Fry (1947) and some of the ecological implications of the observations are considered.

INTRODUCTION

In many lakes throughout Europe and North America pulses of different classes of algae succeed one another in a regular seasonal cycle (Berg and Nygaard, 1929; Chandler, 1940, 1942, 1945; Lund, 1948, 1949, 1950; Rodhe, 1948, 1949; Spencer, 1950; Verduin, 1951). In this cycle the diatoms and yellow-green flagellates dominate the phytoplankton during the spring and autumn, whereas green and blue-green algae predominate in summer. In general all classes become scarce with the onset of winter, though Rodhe (1955) reports that certain minute green algae appear to flourish in subarctic lakes during the winter.

The regularity with which the seasonal cycle of algal pulses occurs has led many investigators to try to relate it to a seasonal change in some aspect of the

[1]Received for publication April 26, 1960.

[2]Condensed from a thesis presented to the University of Toronto in partial fulfilment of the requirements for the Degree of Doctor of Philosophy, which contains the numerical data on which the figures presented here are based.

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environment. Some workers have suggested that this cycle is the result of changes in water temperature (Daily, 1938; Damann, 1943, 1945; Spencer, 1950). Others have concluded that a seasonal change in nutrient supply is a major factor causing certain classes of algae to flourish at one time of year and decline at another (Pearsall, 1923; Chandler, 1940, 1942, 1944, 1945; Chu, 1942, 1943; Lund, 1948, 1949). A third group has argued that each class of alga may have a characteristic tolerance for light intensity and that the seasonal succession of pulses is caused by seasonal changes in solar radiation (Findenegg, 1943; Wohlschlag and Hasler, 1951). However, although one particular factor may give a conspicuous correlation with the numbers of algae in a given instance, we must realize that the metabolism and growth of an algal population is really a complex function of all three factors considered (Riley, 1939, 1943; Riley and von Arx, 1949; Tamiya *et al.*, 1953). The importance of the interaction of temperature and light intensity on the photosynthesis of phytoplankton has been demonstrated recently by Talling (1957a, b) for several species of freshwater diatoms in culture and in lakes.

A study of the effects of an inorganic fertilizer on the phytoplankton of certain lakes in Algonquin Park, Ontario (Langford, 1949; McCombie, 1951) suggested that each of the three factors, temperature, light intensity and nutrient concentration played a specific role in the development of algal pulses. Fertilizing the lakes caused large increases in abundance of all major classes of phytoplankton present, but it was evident that the forms which responded to fertilization at a given time were those favoured by the temperature at that time. In contrast, cloudy weather (reduced light intensity) prevented or terminated the development of pulses, even though the temperature and nutrient conditions favoured growth.

In the present work cultures of the green alga *Chlamydomonas reinhardi* Dangeard were used to investigate the roles of temperature, light intensity and nutrient concentration in the growth of phytoplankton. The experiments were designed to demonstrate the action of temperature as a *controlling factor* and of light intensity and nutrient concentration as *limiting factors* in such a way as to show the interactions of these three factors on the growth of the alga.

The terms limiting and controlling factors as used in this work have meanings which were carefully defined by Blackman (1905) and Fry (1947). Blackman recognized that such factors as light intensity and nutrient (carbon dioxide) supply govern the rate of metabolism by determining the amount of material available for it. Hence he termed such factors *conditions of supply*. He also pointed out that there were other aspects of the environment, such as temperature, which affect the rate of metabolism by determining the state of activation of the molecules taking part rather than by restricting the supply of energy or material. The latter factors he called *tonic conditions*. However, although Blackman realized that the environmental factors should be divided into two categories, he did not recognize the full magnitude of the difference between their roles, and he grouped them both under the heading of limiting factors.

The true magnitude of the difference between tonic conditions and conditions of supply continued to escape notice until comparatively recently, when they

were brought out by Fry (1947). He pointed out that tonic conditions differ fundamentally from conditions of supply in that the former influence both the active and standard metabolism whereas the latter affect only the active level. In other words, tonic conditions control the maximal rate at which an organism *can* metabolize and also the minimal rate at which it *must* metabolize: conditions of supply govern only the maximal rate. In addition Fry noted that several tonic conditions must act concurrently, whereas conditions of supply may act singly or concurrently in the manner suggested by Blackman. He proposed therefore to apply the term *controlling factor* to the tonic conditions and to reserve the term *limiting factor* for conditions of supply. This practice is followed in the present work.

Besides distinguishing between limiting and controlling factors, Fry (1947) carefully defined several other categories of environmental factors into which he considered the environmental conditions could be put. His definition of an *accessory factor* will be given later when the evidence for such a factor in the alga cultures is considered.

The immediate points to be demonstrated in this work are as follows. The scope for growth activity of an alga is equal to the difference between the rates of photosynthesis and respiration, which may be considered analogous to active and standard metabolism respectively. Temperature acts as a typical controlling factor, governing the rate of growth by determining the rates of both the active and standard metabolism simultaneously. The actual rate of growth at any temperature is, nonetheless, dependent upon the effect of the limiting factor as well as on that of the controlling factors. The light intensity or nutrient supply may play the typical role of the limiting factor, which determines the scope for activity by regulating the rate of photosynthesis or active metabolism. In addition, the concentration of nutrient salts appears to act as an *accessory factor*, reducing the potential temperature range for activity and shifting the temperature for optimum growth.

ACKNOWLEDGMENTS

It is a pleasure to acknowledge the guidance and support of my supervisor, Dr R. R. Langford, and of Dr F. E. J. Fry who first aroused my interest in the aspects of physiological classification dealt with in this work. The stimulating introduction to plant physiology given by the late Dr G. H. Duff and by Dr Dorothy F. Forward is also gladly acknowledged. Many thanks are due to Dr K. C. Fisher for his advice on the culture and physiology of microorganisms, to Dr L. Butler for his help with the statistical aspects of the problem and Dr J. Murray Speirs for help in editing the manuscript. For the identification of the organism, I am much indebted to Dr C. Mervin Palmer of the Robert A. Taft Sanitary Engineering Centre, Cincinnati, Ohio.

This investigation was carried out in the Ontario Fisheries Research Laboratory of the Department of Zoology at the University of Toronto. Financial support for the earlier stages of the work was provided from funds for limnological

research granted by the National Research Council of Canada to Dr J. R. Dymond, at that time head of the Department of Zoology. The final stages were supported by a studentship and summer supplement awarded to the writer by the Fisheries Research Board of Canada.

MATERIALS AND METHODS

The strain of *Chlamydononas reinhardi* Dangeard used in this investigation was isolated from a water sample taken from Sturgeon Lake, Victoria County, Ontario. The genus *Chlamydononas* has two distinct phases, namely: a free-swimming, flagellated, unicellular phase and a non-flagellated, multicellular palmelloid phase in which the cells remain embedded in a common matrix formed by the gelatinization of the parent cell walls. In either phase the cells grow and reproduce actively when exposed to suitable temperature, light and nutrient conditions. In the present work the alga took on the palmelloid form in both agar and liquid media. On the solid medium, it grew in continuous sheets, whereas in the liquid it formed small clumps. Motility was induced in one or two instances by keeping the organism in tightly stoppered vials for a few days.

In order that the organisms used in the experiments would always have the same history, stock cultures were maintained continuously under constant temperature and light conditions. Fresh stocks were started regularly every 10 or 11 days to avoid serious reduction in nutrient supply or accumulation of waste products. Four stock cultures were maintained at a time and at the end of the 10- or 11-day interval, those stocks which were in good condition were thoroughly mixed together and aliquots were then withdrawn to inoculate new stock cultures.

The inocula used to initiate experimental cultures were withdrawn from the pooled stocks at the same time that the fresh stock cultures were started—that is, at the end of the 10-day interval. It is important that the inocula be always in the same state, because inocula which differ in this respect may respond quite differently when introduced into a given experimental environment (McCombie, 1953).

The stock cultures were grown in 1-litre Erlenmeyer flasks kept in a light-tight cabinet and continuously illuminated by 2 neon tubes (Ketchum and Redfield, 1938). The distance between the centres of each flask and the neon tubes was 25 cm. The temperature in the cabinet was controlled by a heater and thermostat, and with the exception of one or two periods when the room temperature was very high, it remained at $27 \pm 2°$[4]. The culture medium was the iron citrate modification of Chu's No. 10 solution (Rodhe, 1948). A stream of air bubbles kept the algae in suspension. This air was passed through sterile cotton batting to remove dust and bacteria and through a tall column of water to humidify it before it entered the cultures. Fifty millilitres of culture containing about 500,000 cells per ml were used to inoculate 1 litre of culture medium.

[4]All temperatures in this paper are in degrees Centigrade.

The cultures used in the experiments were raised in 2 temperature control baths enclosed in light-tight compartments and illuminated continuously with white fluorescent light. These cultures were grown in bacteriological flats of about 500 ml capacity. Each culture consisted of 25 ml of inoculum (500,000 cells/ml) and 250 ml of the iron citrate modification of Chu's No. 10 solution. Each flask was closed with a rubber stopper which was provided with a glass tube of 5 mm bore plugged at its outer end with non-absorbent cotton to allow for gas exchange with the atmosphere. The flasks were placed horizontally across rocking shelves, which were suspended just below the surface of the water baths so that the surface of the liquid in the cultures was level with the water in the baths when the shelves were in the horizontal plane. The shelves moved at 24 strokes per minute through a total arc of 15 degrees.

One of the baths could be set at any particular temperature within the range 8° to 20° while the other could be kept at any temperature between 20° and 35°. Five replicates were accommodated in each bath. Ordinarily the temperature in the baths did not vary more than ±2° during the course of an experiment. In a few cases, however, the thermoregulator failed to work and the temperature rose or fell 4° to 5° overnight. These larger variations were taken into account when the results of the experiments in question were interpreted.

The intensity of the light reaching the culture flasks was changed by altering the distance of the light source from the cultures and was measured in the plane of the surface of the culture medium with a General Electric Model 8DW40Y16 light meter. This instrument was calibrated in foot-candles (f-c) and was compared with a Weston Model 756 light meter from time to time. There was a light gradient along each shelf such that the intensity was 15% to 20% greater at the middle than at either end of the shelf. The light intensities given in this paper are averages of readings made at the middle and both ends of each shelf.

Measurement of Population Density

At intervals of from 1 to 3 days, each flask of experimental culture was vigorously shaken and a 3-ml sample was withdrawn from it. This sample was subdivided into 3 equal parts, each of which was diluted with an equal amount of distilled water. From each of the parts in turn, a 1-ml subsample was withdrawn and transferred to a Sedgwick–Rafter counting chamber. This chamber was then examined under a compound microscope at a magnification of × 200. The number of cells in each of 20 optic fields of the microscope was then recorded for each subsample. The population density, in cells per ml, was then calculated from these cell counts.

RESULTS

The Sigmoid Curve of Growth

When cell counts were made at frequent intervals throughout the life of a culture of *C. reinhardi* and plotted against time on arithmetic paper, the data lay on a sigmoid curve (Fig. 1). This type of curve is characteristic of populations

reared in a restricted space or on a fixed amount of medium. It is well known from studies on cultures of bacteria, yeasts, fungi and protozoa. Pratt (1940, 1942, 1943, 1944), Rodhe (1948), Lund (1949) and others have also encountered it in culturing planktonic algae.

Of the several mathematical treatments proposed for the sigmoid curve of growth (e.g., Robertson, 1923; Thompson, 1942; Clark and Medawar, 1945;

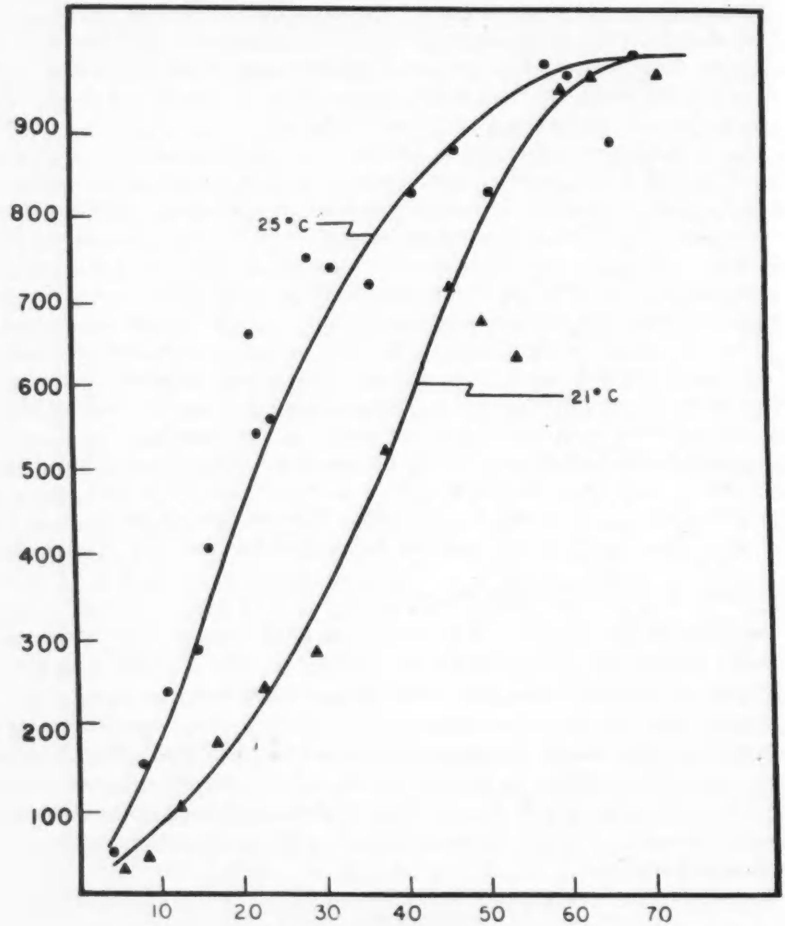

FIG. 1. Examples of the sigmoid growth curve for cultures of *C. reinhardi*. In these two experiments the nutrient medium was used at standard strength and the illumination was 150 f-c. Only the temperatures differed. (Ordinate scale—thousands of cells per ml.)

Andrewartha and Birch, 1954) the one adopted here is probably the simplest. It is commonly used in bacteriology and has also been applied to studies on unicellular algae in cultures by Myers (1953), Spencer (1954) and others. In this treatment the sigmoid curve is first divided into sections depicting (a) an initial lag phase of growth which may be lacking in some cases, (b) a logarithmic phase and (c) a final senescent phase. The measure of growth is then derived from that part of the curve corresponding to the logarithmic phase. The sigmoid curve of growth for the present cultures of *C. reinhardi* can be divided into two parts representing the logarithmic and senescent phases.

In the logarithmic phase, growth obeys the "compound interest law" which can be stated by the formulae:

$$P = P_0e^{kt}, \text{ or } \log_{10}P = \log_{10} P_0 + 0.434\, kt \; . \; . \; . \; . \; . \; (1)$$

Here P represents the concentration of cells at any time, t; P_0 represents the concentration at the time of inoculation; e stands for the base of the natural logarithms; and k is the *growth constant.* The growth constant k is regarded as the best measure of growth to use in the present type of study for two reasons. First, k appears to represent the innate capacity of the organism to multiply under the conditions presented by the experimenter (see for example Myers, 1953). Secondly, k is equal to the specific growth rate:

$$\frac{dP/dt}{P}$$

(Clark and Medawar, 1945), which expresses the increment in growth for any interval as a fraction of the amount of growing material present in that interval.

There is another reason why we should focus our attention on the logarithmic phase of growth in the present work, where the measure of growth is based upon the increase in cell number. As von Witsch and Harder (1953) have shown for *Nitzschia palea* and *Chlorella pyrenoidosa*, the alga is most likely to convert its metabolic product into new cells during the logarithmic phase of growth. Accumulation of storage material, which would not be measured by cell counts, is likely to be minimal in this phase. On the other hand, these authors have found that in the senescent phase of culture the metabolic product becomes channeled into the formation of storage products. Under the latter conditions growth would have to be measured by change in volume or weight rather than change in number of cells.

Figures 2 to 5 display the results of the individual experiments and show how closely the data lie along the line of best fit described by (1). The experiments are grouped according to the nutrient concentration and light intensity used. In about 45% of the experiments the data lie on or quite close to the line and the goodness of the fit is obvious (solid lines in the Figures). In another 27% the data deviate considerably from the line, but the fit is still good (dashed lines in the Figures). The data in the remaining experiments appear, on first observation, to follow curved lines. A scrutiny of the temperature and light

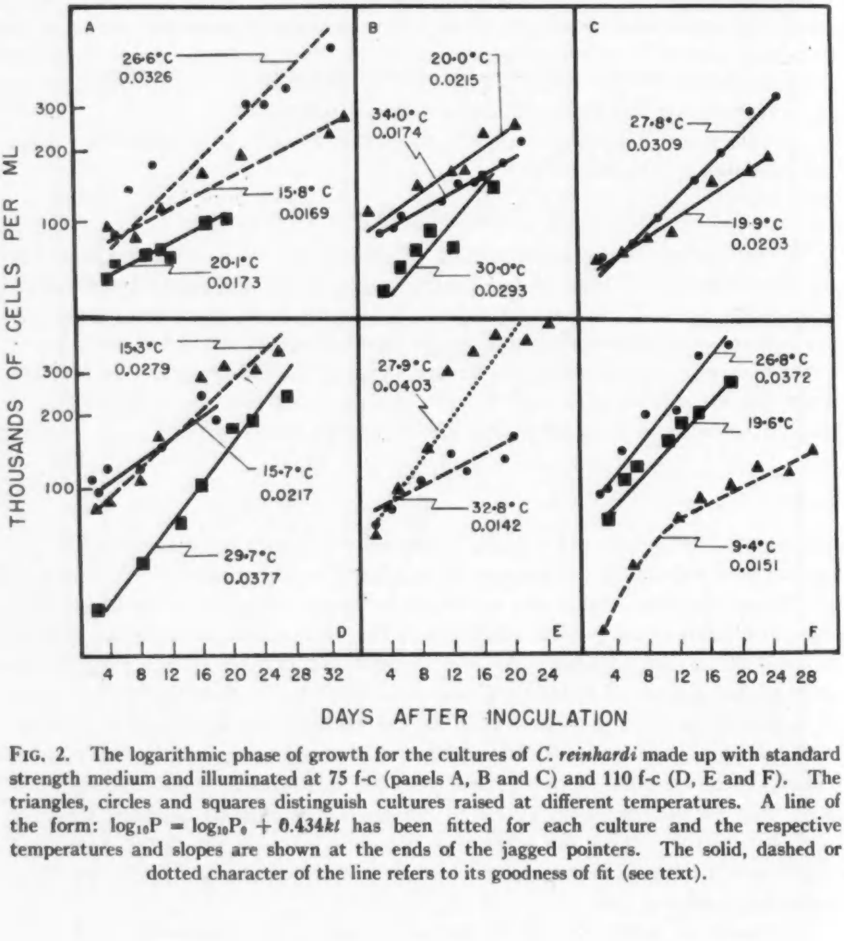

FIG. 2. The logarithmic phase of growth for the cultures of *C. reinhardi* made up with standard strength medium and illuminated at 75 f-c (panels A, B and C) and 110 f-c (D, E and F). The triangles, circles and squares distinguish cultures raised at different temperatures. A line of the form: $\log_{10}P = \log_{10}P_0 + 0.434kt$ has been fitted for each culture and the respective temperatures and slopes are shown at the ends of the jagged pointers. The solid, dashed or dotted character of the line refers to its goodness of fit (see text).

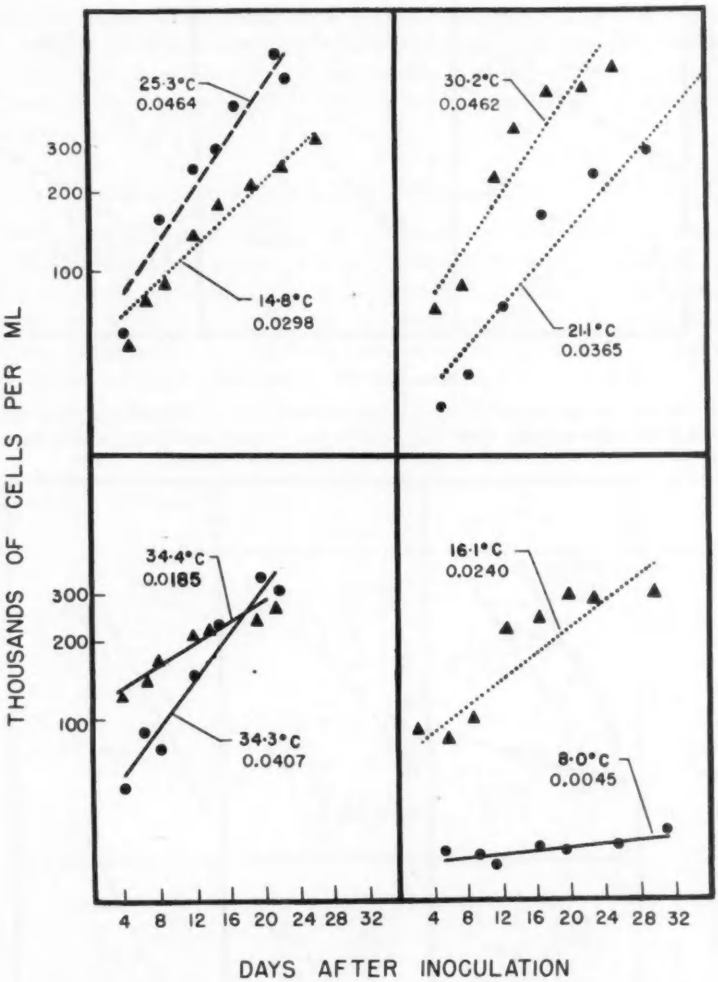

FIG. 3. The logarithmic phase of growth for *C. reinhardi* maintained at different temperatures in standard strength medium at 150 f-c illumination: details of display as in Fig. 2.

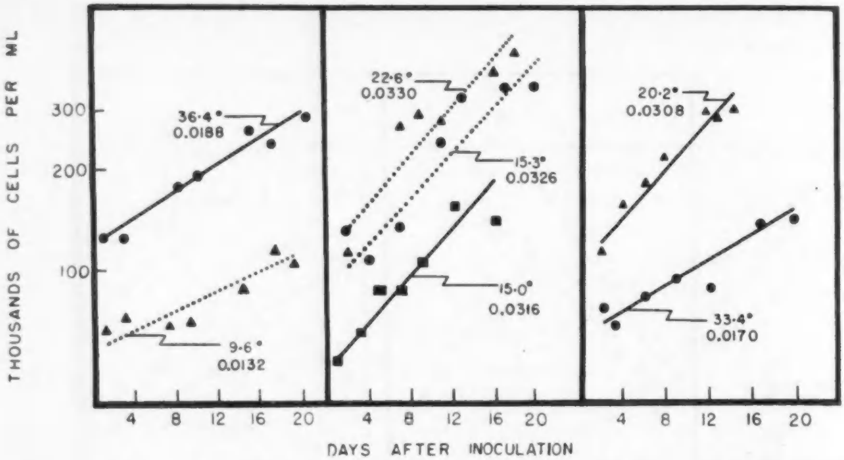

FIG. 4. The logarithmic phase of growth of *C. reinhardi* cultured at different temperatures in standard strength medium under 200 f-c illumination: details of display as in Fig. 2.

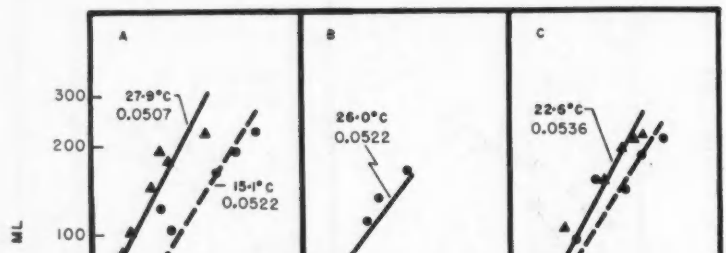

FIG. 5. The logarithmic phase of growth of *C. reinhardi* cultured at different temperatures in double strength medium at 200 f-c illumination: details of display as in Fig. 2.

intensity records for these last experiments fails to reveal any cause for curvature. Moreover, there is no consistent pattern in the curves. They may appear hyperbolic or sigmoid, and the curves in some experiments are the reverse of those in others. It seems reasonable, therefore, to conclude that these curvatures are artifacts arising out of sampling or possibly counting errors and that, even in this last group of experiments, the data are best described by straight lines (dotted lines in the Figures).

Relation Between Growth Rate and Temperature

The first series of experiments, the growth–time curves of which are shown in Fig. 3, was performed to determine the general relation between the specific growth rate of *C. reinhardi* and temperature. Eight sets of 5 cultures each were raised at different temperatures over the range 8° to 35°, while the light intensity was kept at 150 f-c and the nutrient medium was used at the concentration recommended by Rodhe (1948). This nutrient concentration will be referred to as "standard strength" in following sections. The specific growth rates (k) for this series are plotted against temperatures in Fig. 6[5].

[5]Note that the slopes given for the lines in Fig. 2–5 are equal to 0.434k, since the cell counts are plotted on a base-10 logarithmic scale.

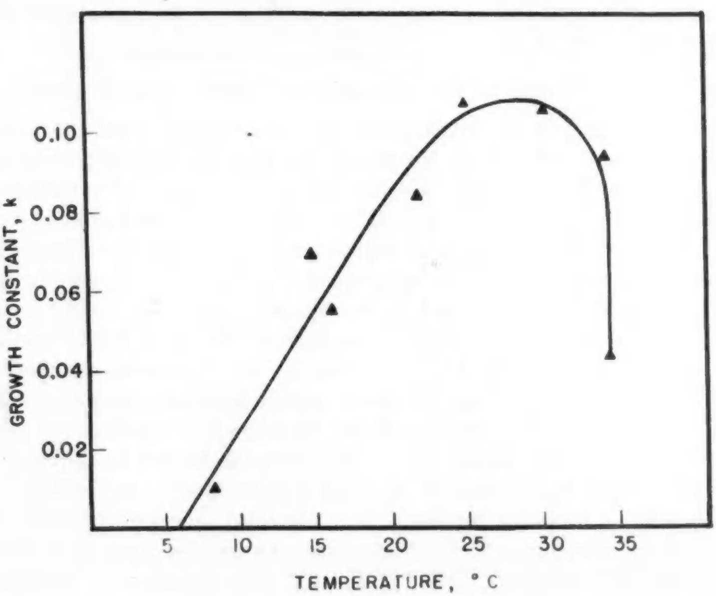

FIG. 6. The relation between the specific growth rate or growth constant (k) of *C. reinhardi* and temperature, in the experiments with standard strength nutrient and 150 f-c illumination.

The lowest observed value of k was negligible, namely 0.010 at 8°, and extrapolation of the growth–temperature curve suggests that there would be no growth at all below 6°. Above 8° the value of k increased as the temperature increased until it reached a maximum at about 28°. With further increase in temperature k declined gradually until the temperature reached 34° or 35°. At the latter level the situation is confusing at first sight because the last two points on the curve suggest that the alga grew at two quite different rates, even though the temperature regime appeared to be the same for the experiments represented by these points.

It is evident that a difference of 1 or 2 degrees Centigrade in the neighbourhood of 35° makes a great difference in the growth of this alga and the apparent confusion referred to above is due to irregularities in the daily temperatures which cannot be seen in the averages for the whole period. In the experiment which gave the point $k = 0.094$ the temperature remained around 34° or 35° throughout most of the experiment: it approached 36° only during the last 3 days of the experiment. In contrast, in the experiment which gave the point $k = 0.041$ the temperature rose as high as 36° and 37° during the first half of the experiment (i.e., on the 4th and 10th days respectively). The picture at the upper end of the growth–temperature curve for the first series of experiments seems, therefore, to be that the specific growth rate declined gradually between 28° and 34° and then dropped off sharply at 35°. The series of experiments with 110 f-c illumination, discussed below, show further evidence of this precipitous decline in growth rate at 34° or 35°.

Effect of Light Intensity on the Growth–Temperature Relation

The second step in this investigation was to determine what effect changes in light intensity would have on the relation between the specific growth rate of *C. reinhardi* and temperature. To this end 3 more series of experiments at various temperatures between 8° and 35° were performed with standard strength nutrient but with the light intensity changed to 75, 110 and 200 f-c respectively. The growth curves for these series are given in Fig. 2 and 4, while specific growth rates derived therefrom are plotted against temperature in Fig. 7 and 8.

The effect of reducing the light intensity from 150 f-c to 110 f-c and 75 f-c can be seen on comparing the 3 curves in Fig. 7. The uppermost of these curves illustrates the relation between the specific growth rate and temperature at 150 f-c and is the same curve as given in Fig. 6: the lower two represent the growth–temperature relations at 110 and 75 f-c. When the line for 110 f-c is extrapolated back to the abscissa it appears that, as in the experiments at 150 f-c, there would be no growth at temperatures below 6°. Moreover, the growth–temperature curve for the experiments at 75 f-c could also be extrapolated back to 6°, provided the point for the experiment carried out at 13° were disregarded. Grounds for disregarding this point would be that it indicates a complete failure in growth which might well be due to some factor other than weak light and low temperature. Above 6° the curves for the experiments at 110 and 75 f-c rise until they reach

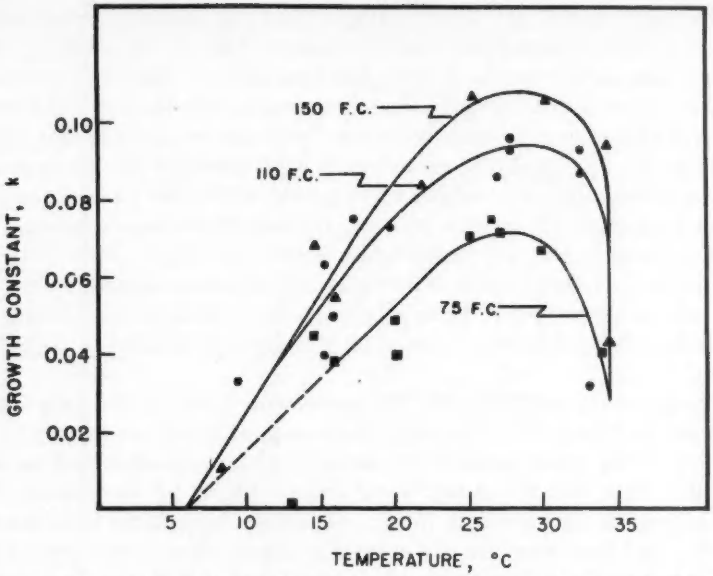

FIG. 7. The relation between the specific growth rate (*k*) of *C. reinhardi* and temperature in the experiments with standard strength nutrient and light intensities of 150, 110 and 75 f-c.

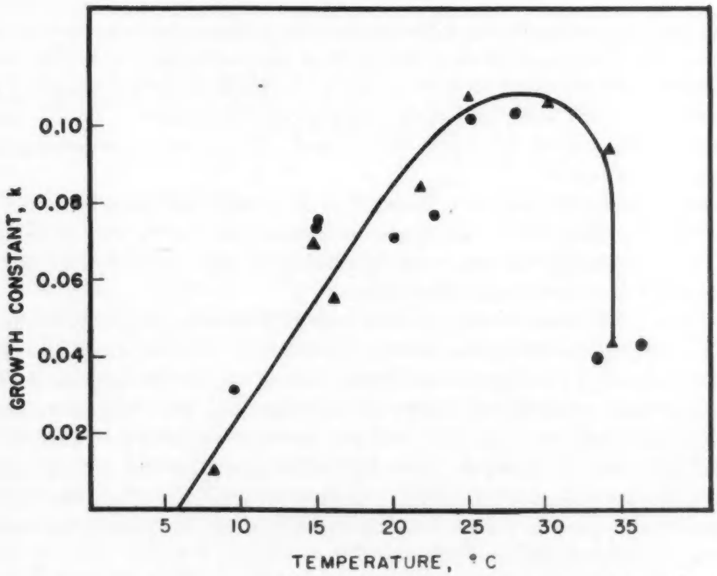

FIG. 8. The relation between the specific growth rate (*k*) of *C. reinhardi* and temperature in the experiments with standard strength nutrient medium and light intensities of 150 and 200 f-c. The same line appears to fit the data for both experiments.

their peaks at about 28°, which indicates that the optimum temperature for these two series of experiments was the same as that for the series at 150 f-c. However, the highest specific growth rate attained was roughly proportional to the light intensity in each case. At supra-optimal temperatures the curves for 110 and 75 f-c decline and appear to converge with that for 150 f-c as they approach the 35° level. Evidently the reductions in light intensity did not appreciably alter the temperature range within which growth could take place or the general form of the growth–temperature relation, although it did cause a decrease in the specific growth rate at any temperature within the range. Hence, the effect of the reduction in light intensity on the growth–temperature relation of *C. reinhardi* was the typical effect which a lowering in the level of the limiting factor has on the relation between a rate of an activity and the level of a controlling factor.

The specific growth rates for the experiments in which the light intensity was raised to 200 f-c while the nutrient was kept at standard strength are compared with those for the experiments with 150 f-c and standard medium in Fig. 8. It is evident that the results of the series with 200 f-c were essentially the same as those for the series with 150 f-c. Therefore, some factor other than light intensity must have restricted the growth in the experiment with 200 f-c. The possibility that the concentration of nutrient salts was the factor responsible was investigated in the series of cultures to be described next.

Effect of Nutrient Concentration on the Growth–Temperature Relation

In the final series of experiments the concentration of nutrient salts was doubled while the light intensity was kept at the same level as in the series of experiments just described, namely at 200 f-c. Again, as in the foregoing series, cultures were raised at several temperatures over the range 8° to 35°, and the resulting specific growth rates were determined. These rates are plotted against temperatures in Fig. 9.

When the concentration of salts supplied to an organism is markedly increased there may, of course, be some danger of plasmolysis. However, it seems unlikely that this dangerous level was approached in the cultures described here, even though the concentration was doubled.

Doubling the concentration of salts caused appreciable changes in the form of the growth–temperature relation for *C. reinhardi*. One of these changes was that the curve rose to a higher maximum than it did for the experiments with standard strength medium and 200 f-c illumination (Fig. 9). Thus the maximum value for k attained in the double strength medium was 0.13 as compared with 0.11 for the standard strength. The fact that increasing the concentration of nutrient salts caused this acceleration in growth confirmed the belief that the nutrient supply was the factor limiting growth in the cultures with standard strength medium and 200 f-c light intensity.

Another way in which the increase in concentration of nutrient salts affected

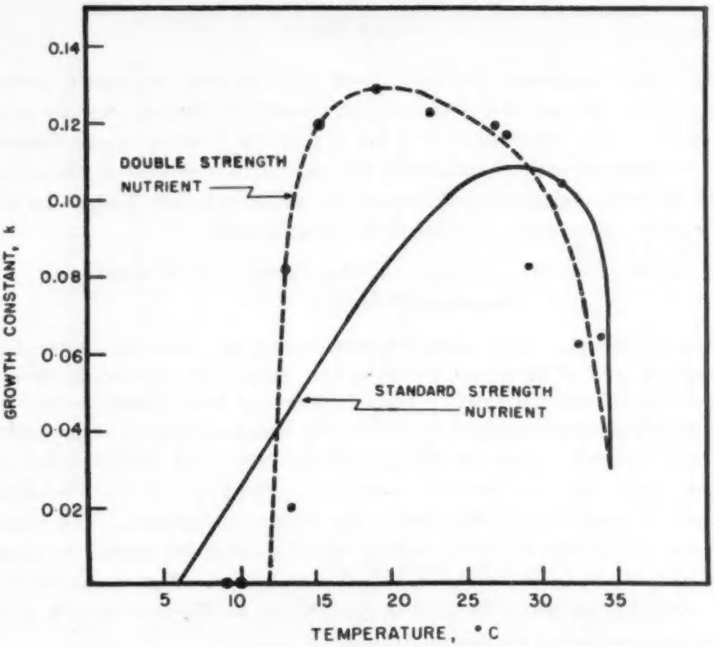

FIG. 9. Effect of doubling the concentration of all salts in the medium on the growth–temperature relation of *C. reinhardi*. The dots represent data for the cultures with double salt concentration and 200 f-c illumination: the curve with the higher peak is fitted to these. The curve with the lower peak is the same as the one shown in Fig. 8 for the cultures with standard salt concentration and light intensities of 150 and 200 f-c.

the growth–temperature relation of *C. reinhardi* was that it reduced the range of temperature within which growth took place. Specifically, it raised the lower limit of this range from the 6°-level found in the experiments with standard strength medium to about 12° (Fig. 9). This shortening of the range indicates that the increased salt concentration played some additional role which offset its accelerating effect on photosynthesis growth at temperatures below 12°.

The increase in salt concentration also caused a marked shift in the optimum temperature of the alga. In each of the series of experiments with standard strength medium (see Fig. 6 to 8, and also the lower curve in Fig. 9) the optimum temperature was about 28°. In contrast, the optimum temperature for the experiments with double strength medium was about 18° (upper curve in Fig. 9). At temperatures above 18° the specific growth rate for the experiments with double strength nutrient medium decline rapidly so that, at about 30°, it was little different from the rate for the experiments with standard strength.

DISCUSSION

It is usually assumed that the growth which an organism accomplishes in a day is equal to the amount of material it assimilates daily minus the amount it dissimilates in the same period. When a plant is illuminated continuously, as in the experiments with *C. reinhardi*, the assimilatory process of photosynthesis and the dissimilatory process of respiration can be considered to go on simultaneously and continuously. Under such circumstances:

$$\begin{aligned} \text{rate of growth} &= \text{rate of photosynthesis} - \text{rate of respiration} \\ &= \text{net assimilation} \end{aligned}$$

Ideally the quantities in this system should be given in units of energy processed per unit of living matter per unit of time. In practice, however, more readily measured units are used. Thus growth may be expressed in terms of cell counts while photosynthesis and respiration are stated as volumes of gas exchanged.

Photosynthesis represents the maximum amount of energy which *can* be processed under the prevailing environmental conditions. It may be considered analogous to what Fry (1947) terms the active metabolism. The respiration represents the amount of energy which *must* be processed under the same conditions and is analogous to the standard metabolism. Net assimilation is the energy available for activities such as growth and for the cost of such activities. It is comparable to Fry's scope for activity.

The controlling effect of temperature on the respiration and photosynthesis of *Chlamydomonas* is postulated in the curves AB and AC of Fig. 10 respectively. These curves are based on the Q_{10} values published by van der Paauw (1934) and on the fact that he found the rate of respiration to be, on the average, about 27% that of photosynthesis. Unfortunately he did not give absolute rates of gas exchange but the relative values are sufficient for the present considerations.

The respiration curve rises fairly steeply throughout its course whereas the curve for photosynthesis takes a sigmoid form, rising steeply over the temperature range 6° to 25° and then tending to flatten off from 25° upwards. The differences between corresponding ordinates of the curves AB and AC represent the *scope for activity* at successive temperatures. They are plotted in Fig. 11 to give the curve ED. This curve resembles the relation between growth and temperature (Fig. 6) and, according to Fry's concept, it is actually the form of the scope curve rather than that of either standard or active metabolism which determines the form of an activity curve. Since temperature affects the rate of both respiration and photosynthesis simultaneously, it plays the typical role of a controlling factor.

The limiting effect of light intensity on photosynthesis in the classical Blackmanian sense is well known. What is less appreciated is the interaction of this limiting effect with the controlling effect of temperature as illustrated

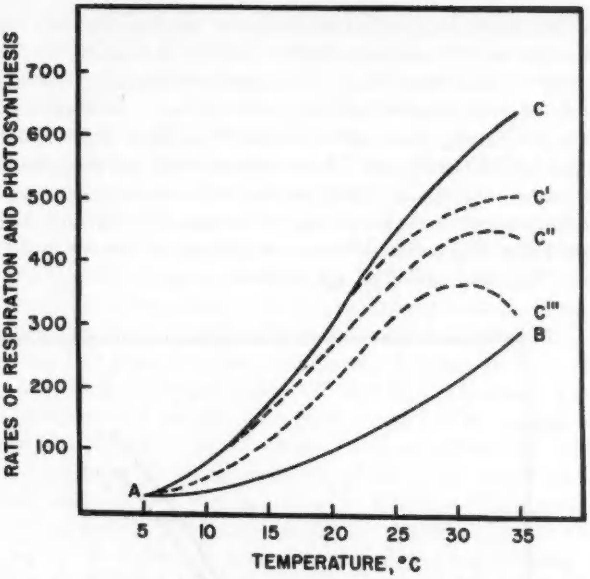

Fig. 10. Curves AB and AC postulate the controlling effect of temperature on the respiration and photosynthesis of *Chlamydomonas* respectively. The rates are relative and that for respiration at 20° is set at 100. Curves AC′, AC″ and AC‴ show the interaction between the photosynthesis–temperature relation and the limiting effect of light at intensities of 150, 110 and 75 f-c respectively.

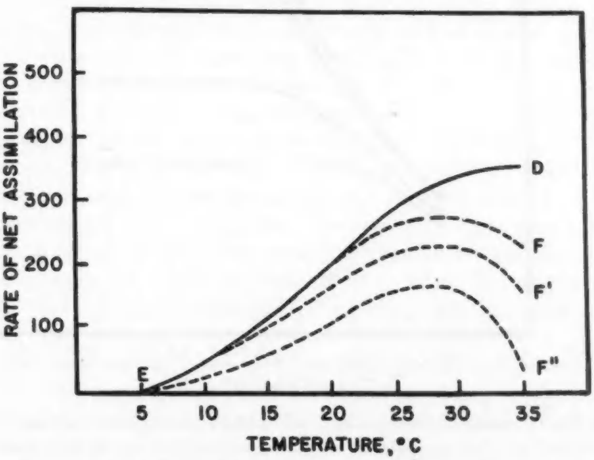

Fig. 11. Curve ED postulates the controlling effect of temperature on the net assimilation of *Chlamydomonas* and curves EF, EF′ and EF″ illustrate the interaction of this controlling effect with the limiting effect of light at intensities of 150, 110 and 75 f-c respectively. The rates are relative.

in Fig. 12. The curves in this figure are based on data derived from the third figure in the paper on the photosynthesis of *Chlorella vulgaris* by Wassink *et al.*, (1938). In essence the reduction in light intensity flattens or lowers the upper portion of the photosynthesis–temperature relation. A similar set of curves AC′, AC″ and AC‴ have been inserted into Fig. 10 to postulate the effect of light intensities of 150, 110 and 75 f-c respectively on the photosynthesis of *C. reinhardi*. The consequent effect on the relation between net assimilation (scope) and temperature is suggested by the curves EF, EF′ and EF″ in Fig. 11, which represent the differences between ordinates of the respiration curve AB and the curves AC′, AC″ and AC″ respectively.

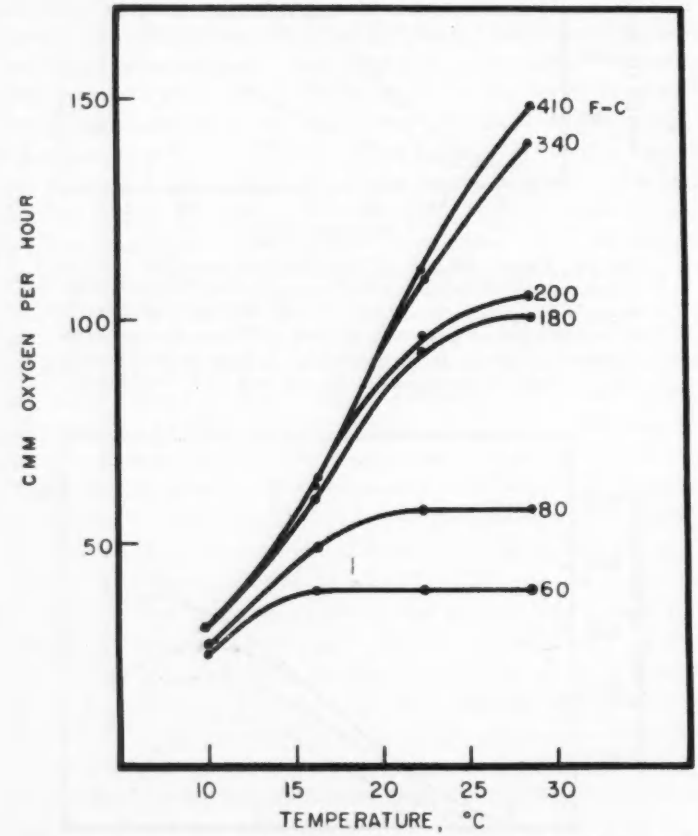

FIG. 12. The relation between the rate of photosynthesis (in mm³ of oxygen per hour) of *Chlorella vulgaris* and temperature, at 5 different levels of illumination. These curves were constructed from data taken from figure 3 of Wassink *et al.* (1939). The datum at the upper end of each curve is the approximate foot-candle measure of the respective illumination.

One result of doubling the concentration of nutrient salts would probably be an acceleration of photosynthesis. For example, Müller and Larsen (1935) found that a twofold increase in the supply of nitrogen salts to leaves of *Sinapis alba* doubled the rate of photosynthesis for that plant. In turn an acceleration of photosynthesis would lead to an increase in the scope for activity and ultimately to an increase in growth rate. In the experiments with *C. reinhardi* a twofold increase in the concentration of salts, including nitrogenous compounds, resulted in a doubling of the growth rate at 18° (Fig. 9). When it governs growth through its effect on photosynthesis, the nutrient concentration plays the typical role of the limiting factor. It seems reasonable to suppose, therefore, that the effect of a change in nutrient concentration on the photosynthesis–temperature relation is similar to that of a change in light intensity suggested in Fig. 10 and 11.

However, the fact that the growth in double strength medium was not twice as fast at temperatures above and below 18° and that there was no growth below 12° indicates that the alga did not gain in scope for activity at all temperatures within its tolerance range. The increase in salt concentration must have had another effect besides accelerating photosynthesis. The reduction in the range of temperature tolerance of *C. reinhardi* in the double strength medium suggests the action of what Fry (1947) terms an *accessory factor*. Such a factor cuts off the extremities of the tolerance range by imposing an additional load on the standard metabolism and raising the standard metabolism–temperature curve. In the experiments with double strength medium it is conceivable that the respiration–temperature curve was raised, for it is well known that the uptake of ions by plants requires the expenditure of respiratory energy (Lundegårdh and Burström, 1933, Lundegårdh, 1955; Hoagland and Broyer, 1936; Robertson and Wilkins, 1948; Harley *et al.*, 1956).

On the other hand, many trace elements are toxic when present in anything but the minutest amounts and, since the concentrations of such elements were doubled in the experiments in question, it is possible that the rapid decline in growth rate at temperatures above 18° was due to a differential poisoning. Ions which were present in toxic concentrations might have penetrated the cells more rapidly at the higher temperatures and thus have exerted a greater inhibitory effect at such temperatures. If such an inhibitory effect were being exerted, it might be expected to become greater with the passage of time as the toxic ions accumulated within the cells. Accordingly, there should be a falling off in the growth–time curves for the experiments with double strength nutrient and higher temperatures. It is evident though, that the curves in question (Fig. 5) do not show any appreciable falling off throughout a period of at least 12 days.

These experiments with *C. reinhardi* demonstrate clearly the need for further studies on the role of temperature as a controlling factor in algal metabolism and growth. It is obvious that the effects of limiting factors such as light intensity or nutrient supply can be properly assessed only when they are studied in conjunction with the controlling effect of temperature. If the effects of light or nutrients are determined at a single temperature, as has usually been done, the

results will have a restricted application, since two studies on the effects of light or nutrient conditions made at two different temperatures may give quite different results.

Finally, the following inferences could be drawn about the ecology of *C. reinhardi* from the present work. It seems unlikely that this alga would multiply during the winter when the water temperature is below 6°. It is also unlikely that lakes in the Temperate Zone warm to temperatures above the range for activity of this alga (i.e. above 35°). On the other hand, the fact that this species did show some growth between 6° and 12° is consistent with the observation that *Chlamydomonas* and other unicellular green algae may form layers on the bottoms of shallow pools shortly after the ice breaks up. The chance that *C. reinhardi* will multiply rapidly enough to form a pulse or bloom increases greatly as the temperature reaches 18° to 28°. It also increases as the light intensity or nutrient concentration rises. The long periods of clear weather and high light intensities, which characterize the summer climate in the Temperate Zone, are likely to be most favourable to the growth of *C. reinhardi* when the water temperature is about 28°. In contrast, higher concentrations of nutrient salts appear to be most favourable to growth at temperatures around 18°.

SUMMARY

Experiments were carried out to determine the rate of growth of the planktonic green alga *Chlamydomonas reinhardi* at four different light intensities and two different concentrations of nutrient salts at temperatures over the range 8° to 35°. The nutrient medium used was a modification of Chu's No. 10 solution with iron citrate and citric acid substituted for the iron chloride, as recommended by Rodhe (1948). White fluorescent light was used at intensities of 200, 150, 110 and 75 f-c respectively for the experiments.

The stock cultures were maintained at a constant temperature under continuous illumination with neon light and were restarted in fresh medium every 10 days. Inocula for the experimental cultures were always withdrawn from stocks which were 10 days old.

Growth was measured by direct counts of the increase in cell concentration. The index of growth chosen was the *specific growth rate*.

The general relation between the specific growth rate and temperature is what Fry (1947) considers to be the typical relation between the rate of an activity and the level of a controlling factor.

The growth–temperature curves for the experiments with standard strength medium and light intensities of 200, 150, 110 and 75 f-c indicate that the temperature range for growth under such conditions was 6° to 35°. These limits should not be regarded as fixed cardinal points as they sometimes have been. For example, the lower limit of this range shifted from about 6° to 12° when the concentration of nutrient salts was doubled.

With standard strength medium the temperature at which the specific rate of growth reached its maximum value was about 28°. This temperature optimum

is also not a fixed point. In the experiments with 200 f-c illumination the optimum temperature was shifted from 28° to 18° when the concentration of nutrient salts was doubled.

The specific growth at any temperature within the range for growth depended not only upon the controlling effect of the temperature but also upon the level of the limiting factor. Light limited growth at intensities below 150 f-c. Decreases in intensity from 150 to 110 and 75 f-c brought about decreases in the maximum specific growth rate from 0.11 to 0.093 and 0.071 respectively.

Nutrient concentration limited growth when the light intensity was 200 f-c. Increase in the concentration of nutrient salts accelerated growth under adequate light conditions at intermediate temperatures. It also caused the lower limit of the temperature range within which growth took place to shift from 6° to 12° and brought about a shift in the optimum temperatures from 28° to 18°.

A scheme is outlined in which the growth rate of the *C. reinhardi* is related to the rates of photosynthesis and respiration which van der Paauw (1934) obtained when he cultured a species of this genus at different temperatures. This scheme is based on the assumption that:

$$\begin{aligned} \textit{rate of growth} &= \textit{rate of photosynthesis} - \textit{rate of respiration} \\ &= \textit{net rate of assimilation} \end{aligned}$$

The net rate of assimilation equals the metabolic product available per unit time for growth and is analogous to Fry's (1947) scope for activity. When the light intensity or concentration of nutrient salts was the limiting factor, it probably determined the scope by regulating photosynthesis.

However, when the salt concentration was doubled, this factor seemed to have an additional effect beside accelerating photosynthesis: an effect which offset the potential gain in scope at certain temperatures. The possibility is considered that the increased salt concentration acted as an accessory factor demanding a higher rate of respiration from the alga for the uptake of ions.

The need for studies on the controlling effect of temperature when assessing the limiting effect of light or nutrient conditions is clearly demonstrated in this investigation.

Finally, the ecological implications of the results of these experiments with *C. reinhardi* are discussed briefly.

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Biosynthesis of Trimethylammonium Compounds in Aquatic Animals

I. Formation of Trimethylamine Oxide and Betaine from C^{14}-labelled Compounds by Lobster (*Homarus americanus*)[1,2]

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ABSTRACT

The formation of trimethylamine oxide and betaine in lobster has been studied *in vivo* with radioactive carbon. C^{14}-labelled compounds, tested as possible precursors, were administered to lobsters by injection into the abdominal muscle. Incorporation of the tracer into trimethylamine oxide and betaine, isolated from the whole body, was followed after a metabolic period of 24 and 72 hours.

Administration of Na formate-C^{14}, DL-serine-3-C^{14} and glycine-2-C^{14} does not lead to labelling of trimethylamine oxide. L-methionine-methyl-C^{14} was a poor precursor of trimethylamine oxide, compared with choline-methyl-C^{14}. These findings suggest a possible function for choline or a derivative in trimethylamine oxide biosynthesis.

It appears that the formation of betaine in lobster takes place by oxidation of choline rather than by methylation of glycine. Choline-methyl-C^{14} was found to be a very good precursor, whereas glycine-2-C^{14} was not converted to betaine.

INTRODUCTION

The occurrence of trimethylamine oxide is one of the characteristic biochemical features of sea fish and some marine invertebrates. Data on trimethylamine oxide distribution in fish and invertebrates have been recorded by Dyer (1952), who also reviewed literature concerned with the origin and function of trimethylamine oxide in aquatic animals. More recently Wood (1958) noted that trimethylamine oxide was present in only small amounts in the total excreta of marine teleosts. Reported feeding experiments on fish suggest that at least in some species trimethylamine oxide is of endogenous origin (Ogilvie and Warrem, 1957; Hashimoto and Okaichi, 1958 a, b; Okaichi *et al.*, 1959). There is, however, still no evidence concerning the biosynthetic pathway of trimethylamine oxide in fish or invertebrates.

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Betaine is another trimethylammonium compound present in the free state in some species of fish and invertebrates (Kutscher and Ackermann, 1933; Shewan, 1951, 1953), but little is known of its mode of synthesis in aquatic animals.

In the present investigation the biosynthesis of trimethylamine oxide and betaine has been studied with radioactive carbon in the American lobster. It is known that the two compounds constitute an important part of non-protein nitrogenous constituents of the tissue of lobster (Kermack *et al.*, 1955). This communication reports the results of experiments on the incorporation *in vivo* of isotopic carbon from various C^{14}-labelled compounds into trimethylamine oxide and betaine. Compounds associated with the biological synthesis and transfer of the methyl group were tested as possible precursors.

EXPERIMENTAL

Administration of Labelled Compounds to Lobsters

American lobsters (*Homarus americanus*) of both sexes, captured in the Baie de Chaleur, were used for the experiments. Sodium formate-C^{14}, glycine-2-C^{14}, DL-serine-3-C^{14}, L-methionine-methyl-C^{14} and choline-methyl-C^{14} chloride were purchased from the Nuclear Chicago Corp. Each compound was administered in a single dose, in aqueous solution, to two to four lobsters. A uniform amount of radioactivity was given (2 μcuries per 100 g body weight). Interference of the digestive tract bacterial flora was avoided by injecting the compounds into the muscle. Injections were made with a clinical needle into the ventral portion of the first abdominal segment. After injection the lobsters were kept without feeding in aquariums supplied with running sea water. At the end of a metabolic period of 24 or 72 hours the animals were sacrificed. Details on the administration of labelled compounds are given in Table I.

Table I. Administration of C^{14}-labelled compounds to lobsters.

Expt. No.	Weight of lobsters	Metabolic period	C^{14}-labelled precursor	Specific radioactivity	Amount administered per 100 g body weight	
	grams	*hours*		*μcuries/μM*	*μM*	*μcuries*
1*	320 and 358	24	Sodium formate-C^{14}	4.0	0.50	2.0
2	388 and 305	72	Sodium formate-C^{14}	4.0	0.50	2.0
3	353 and 351	24	Glycine-2-C^{14}	3.7	0.54	2.0
4	390	72	Glycine-2-C^{14}	3.7	0.54	2.0
5	410 and 518	24	L-methionine-methyl-C^{14}	5.4	0.37	2.0
6	439	72	L-methionine-methyl-C^{14}	5.4	0.37	2.0
7	294 and 500	24	DL-serine-3-C^{14}	8.5	0.23	2.0
8	410 and 460	72	DL-serine-3-C^{14}	8.5	0.23	2.0
9	407	24	Choline-methyl-C^{14} chloride	2.4	0.84	2.0
10	367	72	Choline-methyl-C^{14} chloride	2.4	0.84	2.0

*The experiments were started on the following dates: June 15, 1959 (1, 2); Sept. 15, 1959 (3, 4); Sept. 23, 1959 (5, 6); Oct. 13, 1959 (7,8); Oct. 14, 1959 (9, 10).

Isolation of Trimethylamine Oxide and Betaine

Lobsters were killed and dissected in a cold room (0 to 2°C). The shell and the first pair of legs, armed with claws, were cut open and blood, muscles and internal organs were collected. The recovered material amounted to approximatively 40% of the body weight. The material originating from one or two lobsters was combined and homogenized for about 3 minutes in a Waring Blendor with an equal volume of ice-cold water. The suspension was treated with an equal volume of cold 10% (w/v) trichloracetic acid and filtered on a Buchner funnel. The extract was concentrated *in vacuo* at below 55°C to a volume of 250 ml (when operating with one lobster). Trichloracetic acid was removed by extracting the solution three times with ethyl ether and by a further concentration *in vacuo* the volume was reduced to 100 ml.

In the next steps the procedure of Friedman *et al.* (1955) was followed with some modifications. The aqueous solution was extracted with 100 ml of phenol saturated with water. Separation of layers was achieved by centrifugation and the phenol phase was collected and washed three times with water. The phenol solution was afterwards shaken with 50 ml of water and 300 ml of ethyl ether. The water phase was collected and after three washings with ethyl ether it was employed as starting material for ion-exchange chromatography.

For preparative purposes of the present investigation, the size of the chromatographic column originally used in the method of Friedman *et al.* (1955) was considerably increased. By employing a column 150 cm long and 1.8 cm inner diameter it has been possible to isolate in a single run 150 to 200 mg of trimethylamine oxide hydrochloride and of betaine hydrochloride. Test runs with pure trimethylamine oxide and betaine served to show the position of the two compounds in the effluent and the loading capacity of the column. The resin used was Dowex 50-X4, 200 to 400 mesh (Dow Chemical of Canada), treated in the manner described by Hirs *et al.* (1954) for chromatographic separation of amino acids. A sample of lobster extract in 1*N* HCl (5 ml) was introduced on a column previously equilibrated with 1*N* HCl. The column was eluted with 1*N* HCl at room temperature. The initial 1200 ml of the effluent was not fractionated; the next 800 ml were collected as 10-ml fractions at a rate of 25 ml per hour. Two columns were operated simultaneously using one fraction collector (Rinco Instrument Co.). Each fraction was evaporated to dryness under an air stream at room temperature. Crystalline residues of betaine hydrochloride and trimethylamine oxide hydrochloride were obtained from fractions between 1500 ml and 1600 ml and between 1750 ml and 1950 ml, respectively. A green oily residue from the fractions between about 1600 ml and 1750 ml (intermediate to those yielding the two compounds) was noted, but in general this material did not interfere. When overlapping occurred the few contaminated fractions were rejected. The combined fractions containing the respective hydrochlorides were dissolved in water, treated with acid-washed charcoal and filtered. On evaporation of the separate filtrates colourless crystals of betaine hydrochloride

and of trimethylamine oxide hydrochloride were recovered and were further recrystallized from ethanol–water (Kojima and Kusakabe, 1955).

The purity of the crystalline compounds was confirmed by ascending paper chromatography. The solvent system used consisted of a mixture of 95 ml of 95% ethanol (v/v) and 5 ml of concentrated ammonia. The modified Dragendorff solution ($KBiI_4$ reagent) was employed for colour development (Bregoff *et al.*, 1953). R_f values of 0.30 and 0.51 were found for betaine hydrochloride and trimethylamine oxide hydrochloride, respectively. No decrease in specific activity occurred when the crystals were redissolved in ethanol–water and precipitated with an alcoholic solution of chloroplatinic acid.

Degradation of Betaine

In some instances betaine was degraded in order to establish the incorporation of C^{14} into methyl groups. The method of Cotte and Kahane (1953) as described by Bregoff and Delwiche (1955) was employed. Trimethylamine formed in the reaction was precipitated with chloroplatinic acid (du Vigneaud *et al.*, 1941).

Determination of Specific Radioactivity

All compounds were converted to CO_2 by wet combustion (Van Slyke *et al.*, 1951). CO_2 trapped in NaOH solution was precipitated as $BaCO_3$ and mounted by filtration on discs of filter paper. Infinitely thick samples of $BaCO_3$ were counted in the Geiger–Muller region using a Model D-47 Nuclear Chicago Corp. gas flow counter provided with a Micromil window. The observed counting rates, corrected for background, are reported in Table II. The specific radioactivity is expressed in counts per minute per infinitely thick planchet (3.8 sq cm) of $BaCO_3$ (Steinberg and Udenfriend, 1957).

Table II. Utilization of C^{14}-labelled compounds for biosynthesis of trimethylamine oxide and betaine in lobsters.

Expt. No.	Metabolic period	C^{14}-labelled precursor	Specific radioactivity found: Trimethylamine oxide	Betaine
	hours		*counts per minute**	
1	24	Sodium formate-C^{14}	Nil	<5
2	72	Sodium formate-C^{14}	Nil	Nil
3	24	Glycine-2-C^{14}	Nil	Nil
4	72	Glycine-2-C^{14}	Nil	Nil
5	24	L-methionine-methyl-C^{14}	<5	35
6	72	L-methionine-methyl-C^{14}	20	15
7	24	DL-serine-3-C^{14}	Nil	<5
8	72	DL-serine-3-C^{14}	Nil	<5
9	24	Choline-methyl-C^{14} chloride	1050	1710
10	72	Choline-methyl-C^{14} chloride	810	1540

*Per infinitely thick planchet (3.8 sq cm) of $BaCO_3$.

RESULTS

The data obtained on utilization by lobster of various radioactive compounds for the formation of trimethylamine oxide and betaine are presented in Table II.

Isotopic carbon from formate-C^{14}, glycine-2-C^{14} and serine-3-C^{14} was not incorporated into trimethylamine oxide. The methyl carbon of methionine was utilized only to a limited extent. After administration of methionine-methyl-C^{14} some radioactivity was found in trimethylamine oxide, especially at the end of a metabolic period of 72 hours. The labelled methyl carbons of choline were incorporated into trimethylamine oxide to a considerably greater extent at metabolic periods of both 24 and 72 hours. The highest activity obtained in experiments with methionine was 40 to 50 times lower than the activity observed after administration of choline.

When formate-C^{14} was administered a very limited labelling of betaine was observed after 24 hours and no activity was found after 72 hours. At both metabolic periods isotopic carbon from glycine-2-C^{14} was not incorporated into betaine. After administration of serine-3-C^{14} isolated betaine had only trace amounts of radioactivity. The labelled methyl carbon of methionine was incorporated to some extent into betaine and more activity was found after 24 than 72 hours. A relatively very high degree of utilization of methyl carbons of choline for formation of betaine was observed at both metabolic periods.

Betaine isolated after administration of choline (Expt. No. 9) was partially degraded and the specific radioactivity of methyl carbons was determined. The obtained data (2750 cpm) indicate that over 95% of the activity present in the molecule was located in the methyl carbons. The methyl carbons of betaine appear to be almost three times more radioactive than the methyl carbons of trimethylamine oxide.

The experimental procedure used permits comparison of the relative efficiency of various compounds as precursors, but provides no basis for quantitative determination of the percentage of conversion, because the total amount of trimethylamine oxide and betaine present in lobsters and losses by excretion were not measured.

DISCUSSION

The ability of lobsters to synthesize trimethylamine oxide is indicated by the incorporation of isotopic carbon into trimethylamine oxide from some of the compounds tested as precursors. When various types of labelled compounds are compared it becomes evident that the best precursor of trimethylamine oxide is choline-methyl-C^{14}. Choline was tested as a possible precursor of trimethylamine oxide in lobster because it is well established that certain bacteria can produce trimethylamine from choline (Dyer and Wood, 1947; Cohen *et al.*, 1947; Eddy, 1953; Hayward and Stadtman, 1960). The ability of animals to convert choline to trimethylamine is not so well established. Urinary excretion of trimethylamine or trimethylamine oxide by mammalian animals after feeding

of choline has been generally attributed to the activity of intestinal bacteria. This view is supported by the experiments of Norris and Benoit (1945). They found that when choline was fed to rats a noticeable increase of urinary trimethylamine oxide occurred, but there was no increase in trimethylamine oxide excretion following intraperitoneal injection of choline. However, it has been reported that when choline-methyl-C^{14} was incubated with slices or homogenates of rat liver, labelled trimethylamine and its oxide were produced (Artom and Cowder, 1950; Artom and Lofland, 1955).

The formation of trimethylamine oxide from choline with trimethylamine as intermediate supposes the existence of a system capable of oxidizing trimethylamine. No data in this respect exist for lobsters but it is known that trimethylamine can be converted to the oxide by man and some animals (Tarr, 1941; Norris and Benoit, 1945).

Choline-methyl-C^{14} was not the only compound yielding radioactive trimethylamine oxide in lobster. Methyl carbon of methionine was incorporated to some extent into trimethylamine oxide, but compared to choline, methionine was a very poor precursor. This suggested strongly that the labile methyl group of methionine is not directly involved in the biosynthesis of trimethylamine oxide. The observed incorporation of tracer is attributed to a participation of methionine in formation of compounds such as choline, which play a more direct role in synthesis of trimethylamine oxide.

When studying the formation of betaine by lobster the main concern was to establish if the compound arises by methylation of glycine or by oxidation of choline. The observed high degree of incorporation of choline compared with absence of labelling after administration of glycine provides support for the formation of betaine from choline.

It is known that the choline can be formed by transfer of methyl groups from methionine to ethanolamine (Meister, 1957) and the incorporation of some tracer into betaine after administration of methionine-methyl-C^{14} is interpreted by this pathway. It cannot be attributed to methylation of glycine because, as already mentioned, glycine itself gave no labelling of betaine.

The biosynthesis of betaine from choline, occurring in lobster, is a biosynthetic pathway already well established in other organisms (Meister, 1957). The pathway is operating when betaine is an intermediate in transfer of the methyl group, as well as when the compound is accumulating in some plants (Bregoff and Delwiche, 1955; Delwiche and Bregoff, 1958). The oxidation of choline to betaine takes place under the action of the choline oxidase system, which involves the action of two enzymes, choline dehydrogenase and betaine aldehyde dehydrogenase (Quastel, 1955). The biosynthesis of betaine in fish and invertebrates has not been studied extensively. It has been proposed in some earlier studies (Kutscher and Ackermann, 1936) that betaine present in some invertebrates is formed by methylation of glycine, but no direct evidence was presented for the reaction.

The conversion of choline to betaine is of special interest in connection with the utilization of choline by lobster for formation of trimethylamine oxide. It has been reported that betaine, like choline, may be metabolized by some bacteria to trimethylamine and trimethylamine oxide (Davies, 1937; Corfield, 1955). The transformation has not been demonstrated in animal tissue. The possibility that trimethylamine oxide might be formed in lobster from betaine rather than more directly from choline must however be considered. The labelling of trimethylamine oxide and betaine after administration of choline does not exclude this possibility; in both experiments with choline, trimethylamine oxide had a much lower specific radioactivity than betaine. From the data obtained in the present investigation it is not possible to establish whether betaine is an intermediate in formation of trimethylamine oxide from choline.

It is worthy to note our failure to find any appreciable labelling after administration of formate-C^{14}, glycine-2-C^{14} and serine-3-C^{14}. It is known that the biologically active one-carbon fragment which may arise from these compounds can contribute to the formation of the methyl group of choline and consequently betaine. On the other hand, formate and glycine are involved in biosynthesis of serine, which after decarboxylation to ethanolamine may participate in formation of the C-2 moiety of choline (Meister, 1957). The utilization of formate-C^{14}, glycine-2-C^{14} and uniformly labelled serine has been observed during the synthesis of choline and betaine in leaf disks of *Beta vulgaris* (Bregoff and Delwiche, 1955; Delwiche and Bregoff, 1958). The authors noted, however, that in some experiments little or no labelling appeared in betaine of leaf disks which actively incorporated radioactivity into choline. An investigation of the incorporation of tracer into choline in lobster would possibly provide a better basis for the interpretation of the metabolism of formate, glycine and serine.

CONCLUSIONS

It may be concluded from the present investigation that in the lobster biosynthesis of betaine takes place by oxidation of choline rather than by methylation of glycine. The ability of lobsters to synthesize trimethylamine oxide is demonstrated. The tracer technique used cannot show the intermediate steps in formation of trimethylamine oxide, but suggests a function for choline, or a derivative like betaine. Methionine and compounds related to the biologically active one-carbon fragment do not appear to be directly involved in the reaction.

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The Effect of Marine Products on the Blood Cholesterol Levels in Man and in Animals. A Review[1]

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INTRODUCTION

ATHEROSCLEROSIS is a major cause of illness and death in many countries. It is a specific disease process, one among the arterioscleroses, and is the chief cause of death in middle-aged American males. It is not surprising therefore to find that the disease has been the subject of intensive research in recent years. It is thought that there is a correlation between diet, the levels of cholesterol in the blood and the incidence of atherosclerosis. Although this correlation has been demonstrated repeatedly in a number of species of animals to be a cause-and-effect relationship, it is impossible to prove likewise in man by direct experimental means. Nevertheless, there is a voluminous literature regarding the control of blood cholesterol levels by means of dietary constituents and by the employment of other procedures such as the injection of various chemicals.

Innumerable papers have been published on the low blood cholesterol levels obtained when vegetable oils are included in the diet, but considering the fact that marine oils, where studied, have been found to be at least as active as vegetable oils in this respect, it is rather surprising to find that they have been studied comparatively infrequently. The work with vegetable oils has been reviewed adequately by several authors, for example Ahrens (1957) and Portman and Stare (1959), so this article will be confined to a review of investigations on the effect of marine oils and other marine products on blood cholesterol levels in both man and animals.

THE EFFECT OF MARINE OILS ON BLOOD CHOLESTEROL LEVELS

These studies can be divided into two sections: (A) investigations on human subjects, and (B) investigations on animals. The human subjects used in various studies have included both those with normal cholesterol levels and those suffering from hypercholesterolemia. The majority of the animal experiments have been carried out with diets which contained cholesterol, either alone or together with other compounds, in order to make the animals hypercholesterolemic.

(A) HUMAN STUDIES. Bronte-Stewart *et al.* (1956) compared the effect on cholesterol levels of adding various animal and vegetable fats, pilchard oil and seal oil to a low fat (3%) diet. These workers found that 100 g per day of pilchard

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oil or of seal oil lowered the serum cholesterol level below that observed with the low fat diet. When 10 boiled eggs per day were fed to the patient under study, the serum cholesterol level increased. This increase was reversed when the eggs were fried or scrambled in 100 g of a highly unsaturated fraction segregated from pilchard oil. Sunflower-seed oil produced a similar effect but it was not so effective as the fraction from the pilchard oil. Keys *et al.* (1957) reported that the addition of 100 g per day of sardine oil to the diet produced lower serum cholesterol levels than those observed when butterfat was the added substance. In this respect the action of sardine oil was similar to corn oil or sunflower-seed oil. Malmros and Wigand (1957) studied the effect of whale oil on human serum cholesterol concentrations. They found that the addition to the diet of 150 g/day of the oil brought about lower cholesterol concentrations than those observed when the oil was omitted from the diet. Ahrens *et al.* (1959) in carefully controlled experiments showed that menhaden oil was at least as effective as corn oil in depressing serum cholesterol levels in human subjects suffering from hyperlipemia and hypercholesterolemia (Table I).

TABLE I. Influence of dietary fat on serum cholesterol levels in human subjects[a]. Mean values ± standard deviation are for successive determinations which varied in number from 3 to 6.

Patient	Dietary fat	Serum cholesterol
		mg/100 ml
30-year-old male	*Ad libitum* diet	504 ± 44
	Corn oil	253 ± 12
	Menhaden oil	158 ± 5
	Corn oil	197 ± 11
38-year-old female	*Ad libitum* diet	499 ± 21
	Corn oil	306 ± 7
	Menhaden oil	305 ± 28
	Corn oil	325 ± 5

[a]Data from Ahrens *et al.*, 1959.

The above reports indicate that marine oils are at least as effective as vegetable oils in producing low serum cholesterol levels in man. This hypocholesterolemic property of marine oils is possessed by oils obtained from both fishes and from mammals such as the seal and the whale.

(B) ANIMAL STUDIES. As mentioned previously, most of the experiments were conducted with animals fed a diet which produced hypercholesterolemia. March and Biely (1959), however, employing chicks fed a normal diet, studied the effects of added herring oil, corn oil, chicken fat, lard, butter and Crisco on serum cholesterol levels. The level in chicks fed herring oil was reported as being significantly ($P<0.05$) lower than that in chicks fed the animal fats and hydrogenated vegetable fats.

Several workers studied the effects of fish oils added to the diet on the blood cholesterol levels in cholesterol-fed chicks. The results of these investigations are shown in Table II. The tallow and vegetable oils produced high cholesterol levels, as did herring oil and sardine oil. On the other hand, lingcod liver oil

TABLE II. Comparative effects of various dietary fats on blood cholesterol levels in cholesterol-fed chicks[3, 4, 5].

Dietary fat supplement	Duration of experiment			
	2 weeks[3]	4 weeks[4]	2 weeks[5]	9 weeks[5]
	mg cholesterol per 100 ml			
10% dogfish liver oil	321	–	–	–
10% ratfish liver oil	262	–	–	–
10% basking shark liver oil	374	–	–	–
10% lingcod liver oil	155	–	–	–
10% halibut liver oil	147	–	–	–
10% herring oil	697	–	–	–
10% cod liver oil	–	286	–	–
10% linseed oil	–	570	–	–
10% corn oil	798	–	–	–
10% tallow	662	–	–	–
8% peanut oil	–	–	879	1081
8% coconut oil	–	–	1025	1061
8% sardine oil	–	–	769	864

[3]Data from Wood and Biely, 1960a.
[4]Data from Dam *et al.*, 1958.
[5]Data from King *et al.*, 1956.

and halibut liver oil brought about low serum cholesterol concentrations. The liver oils from cod, dogfish, ratfish and basking shark were intermediate in their effect. It is interesting to note that the serum cholesterol levels in chicks appear to reach a "steady state" fairly rapidly because the values obtained after 2 weeks on the diets were not too different from those obtained after a 9-week period.

Similar type studies were carried out on rats by Hegsted *et al.* (1957) using sardine oil, butter, vegetable oils and hydrogenated vegetable fats. The sardine oil was found to be the most effective in preventing hypercholesterolemia caused by dietary cholesterol and cholic acid. Hauge and Nicolaysen (1959) and Peifer *et al.* (1960) approached the problem in a slightly different manner. They employed rats which had already been made hypercholesterolemic by dietary means, and measured the ability of fish oils to lower the elevated serum cholesterol level. Hauge and Nicolaysen showed that the cholesterol concentration decreased appreciably when cod liver oil was dosed in amounts 20 to 80 mg/day. Peifer and his co-workers observed similar results with plasma cholesterol levels when menhaden and tuna oils were introduced into the diet. The substitution of tallow for the fish oils produced no such decrease.

The above results show that marine oils in general have the property of producing low blood cholesterol levels in man and in rats and also in chicks fed

a normal ration. When the chick ration was supplemented with cholesterol the effect of the oils was entirely different. Oils such as herring oil which previously possessed hypocholesterolemic properties now had no such effect. On the other hand some oils, notably lingcod and halibut liver oils, produced low serum cholesterol concentrations when incorporated into the diet of cholesterol-fed chicks. The question now arises as to the reason for the hypocholesterolemic properties of the oils. What component of the oil is responsible, and is it the same for all species?

THE ROLE OF UNSATURATED FAT

Bronte-Stewart *et al.* (1956) expressed the view that in man the different cholesterol levels obtained with various fats bore a relation to the proportion of highly unsaturated and saturated fatty acids in the fat concerned. This view was supported by the work of Ahrens *et al.* (1957) which indicated that serum lipid levels were related to the degree of saturation of glyceride fatty acids as measured by the iodine value of the fat. The behaviour of fish oils with respect to serum cholesterol levels in man was in accordance with the above theory because the oils were highly unsaturated and they produced low levels of cholesterol. However, the iodine value of fish oils cannot be used as a measure of the degree of saturation of glyceride fatty acids because marine oils such as dogfish, ratfish and basking shark liver oils contain large amounts of unsaponifiable material (Bailey, 1952) which contribute substantially to the iodine value of the oil as a whole (Wood and Biely, 1960a).

Speculation arose as to whether a particular type of unsaturated fatty acid component of the oil was necessary to obtain a cholesterol depressive action. Kinsell and Sinclair (1957) postulated that the nutritionally essential fatty acids were responsible. This view was discredited by Ahrens *et al.* (1959) using menhaden oil which they showed had a low essential fatty acid content, yet depressed serum cholesterol levels to at least the same extent as did corn oil (Table I), although the latter oil was rich in essential fatty acids.

In rats, as in man, it was the unsaturated fat which appeared to be responsible for the low serum cholesterol concentrations produced by fish oils. Peifer *et al.* (1960) compared the effects of tuna and menhaden oils with those of ethyl esters of various fatty acids (Table III). The cholesterol depressant effect of the fatty acids increased with the degree of unsaturation and the highly unsaturated fish oils were the most effective of all.

Evidence obtained from only one experiment with chicks (March and Biely, 1959) indicated the possibility that unsaturated glyceride fatty acids might have a similar effect in chicks which are fed a normal poultry ration. Further verification of this point will have to be obtained. It is obvious from the results reviewed here that the degree of unsaturation of the glyceride fatty acids is of no importance in determining the serum cholesterol levels in cholesterol-fed chicks. The

TABLE III. Relative ability of some fats and fatty acid esters to lower plasma cholesterol levels in hypercholesterolemic rats[6]. Values are the mean ± the standard error for 7 rats. The mean plasma cholesterol value prior to the feeding of the fats was 318 mg/100 ml.

Dietary additive	No. of double bonds in molecule	Plasma cholesterol
		mg/100 ml
Tuna oil	–	140 ± 35
Menhaden oil	–	169 ± 14
Ethyl linolenate	3	175 ± 21
Ethyl linoleate	2	238 ± 33
Ethyl oleate	1	346 ± 44
Ethyl palmitate	0	370 ± 72
Tallow	–	344 ± 19

[6]Data from Peifer *et al.*, 1960.

hypocholesterolemic factor observed in the latter experiments was some compound or compounds present in lingcod and halibut liver oil but not in herring oil. The identity of the compound was revealed in investigations described below.

THE ROLE OF UNSAPONIFIABLE MATERIAL

The effect of unsaponifiable components of fish oils on serum cholesterol levels was studied in rats by DeGroot and Reed (1959) and in chicks by Wood and Biely (1960b). The oils were fractionated into fatty acid and unsaponifiable fractions respectively, the individual fractions were incorporated into hypercholesterolemic-producing diets, and their effect on serum cholesterol levels was investigated (Table IV). A striking species difference was evident. With rats the cholesterol depressant factor of cod liver oil was located in the fatty acid fraction. This supports the view expressed above that the glyceride fatty acids were responsible for the low cholesterol levels. On the other hand, with chicks

TABLE IV. Ability of oils and fractions thereof to prevent dietary inducted hypercholesterolemia in rats[7] and chicks[8] (mean values for 10 to 12 rats and 16 chicks respectively).

Addition to cholesterol-containing diet	Serum cholesterol (mg/100 ml)			
	Rats	Chicks		
	Cod liver oil	Lingcod liver oil	Herring oil	Corn oil
None	884	192	192	192
Whole oil	205	130	648	784
Unsaponifiable fraction	750	119	237	193
Fatty acid fraction	281	702	618	793

[7]Data from DeGroot and Reed, 1959.
[8]Data from Wood and Biely, 1960b.

a depressant factor was present in the unsaponifiable material of lingcod liver oil but not that of corn and herring oils. The fatty acid portion of lingcod liver oil increased the degree of hypercholesterolemia as did corn and herring oils and their fatty acid moieties. Further investigations (unpublished) showed that this increase occurred only when the lipid material was added to the cholesterol-containing diet. When corn oil was substituted isocalorically for sucrose in the diet no effect on the serum cholesterol levels was observed.

Some of the compounds which are present in the unsaponifiable portion of marine products have been tested for cholesterol-depressant properties, and the results of these studies will now be reviewed.

(A) VITAMIN A. An examination of the hypocholesterolemic properties of various fish oils incorporated into the diet of cholesterol-fed chicks showed that there was a possible correlation between the activity of the oils and their vitamin A content. Wood (1960) employed chromatography on alumina columns to separate the unsaponifiable material from lingcod liver oil into three fractions whose vitamin A content varied widely. The fractions were incorporated into the diets of cholesterol-fed chicks and the hypocholesterolemic activity of the fractions was observed to parallel the vitamin A content (Table V). Wood also tested crystalline vitamin A acetate and vitamin A alcohol and found that these two compounds were both able to reduce the degree of hypercholesterolemia. It seems reasonable to assume, therefore, that vitamin A is at least partly responsible for the cholesterol-depressant action of lingcod liver oil.

TABLE V. Effect of fractions obtained from lingcod liver oil unsaponifiable material on serum cholesterol levels in cholesterol-fed chicks[a]. Each value is the mean value ± the standard deviation for 16 birds.

Addition to cholesterol-containing diet	Main constituent of the fraction	Vitamin A content of the fraction	Serum cholesterol
			mg/100 ml
None	–	–	336 ± 29
Fraction 1	Vitamin A	Large	197 ± 28
Fraction 2	Cholesterol	Small	248 ± 46
Fraction 3	Glyceryl ethers	None	429 ± 116

[a]Data from Wood, 1960.

It has recently been shown by Kinley and Krause (1959) that oral administration of 100,000 I.U. per day of vitamin A acetate for 4 to 6 months reduced significantly the elevated serum cholesterol levels in atherosclerotic human subjects but had no effect on individuals with normal cholesterol levels.

(B) SQUALENE. This compound is a component of certain fish liver oils. It is also a known intermediate in the biosynthesis of cholesterol. The incorporation of small amounts of the compound into the diet of female rats increased the serum cholesterol levels (Okey *et al.*, 1959).

(C) GLYCERYL ETHERS. These compounds are present in fish liver oils. The most commonly occurring ones are batyl, chimyl and selachyl alcohols. They did not by themselves depress serum cholesterol levels in chicks (Wood, 1960) but they might influence the hypocholesterolemic properties of vitamin A in the fish liver oils due to their emulsifying powers (Wood, 1960).

(D) STEROLS. Plant sterols depressed blood cholesterol levels in man (Beveridge *et al.*, 1958) and in animals (Peterson, 1951). Certain forms of marine life such as the invertebrates contain appreciable amounts of sterols (Idler and Fagerlund, 1955; Fagerlund and Idler, 1959) which are different in character from those found in the plant kingdom. These sterols have not yet been tested for hypocholesterolemic activity but it is hoped to do so in this laboratory in the near future.

EFFECT OF A PRODUCT DERIVED FROM SEAWEED ON BLOOD CHOLESTEROL LEVELS

One of the main carbohydrates found in seaweeds is alginic acid which consists of straight-chain β-D-mannopyruronic acid residues linked through the 1,4 positions. When this product is sulphated it forms a compound which is chemically similar to heparin. The latter substance can diminish hypercholesterolemia and decrease the development of atherosclerosis in rabbits (Constantinides *et al.*, 1953) but it is only partially effective in human patients. Moreover, prolonged dosage of heparin is limited by a certain risk of internal bleeding (MacMillan and Brown, 1953). In view of the disadvantages of heparin Constantinides and his group tested sulphated alginic acid and found that the substance abolished lipemia, reduced hypercholesterolemia and inhibited atherosclerosis produced by cholesterol feeding in rabbits without prolonging the blood clotting time (Gutmann and Constantinides, 1955). When the sulphated alginic acid was given to hyperlipemic and hypercholesterolemic human subjects by the intramuscular route in doses of 2.5 mg/kg body weight/day it displayed a far greater antilipemic activity than equivalent amounts of heparin (Constantinides *et al.*, 1960).

CONCLUSIONS

This review has covered investigations on the effect of various marine products on serum cholesterol levels in man and in animals. The question now arises as to how important a role these products can play in the control of cholesterol levels in human beings. The view is sometimes expressed that eating large quantities of fish will keep blood cholesterol levels low. However, many types of commercially available fish such as lingcod, lemon sole, plaice and cod contain at the most a few percent of oil in their flesh. Even in the more oily species such as salmon and herring the oil content is roughly 7 to 10%, although there are large seasonal variations. In order to obtain an oil intake of 100 g/day, which

is the quantity used in the experiments on man, a person would have to consume 2.2 lb of fish with an oil content of 10%. Moreover, since the blood cholesterol level rises as soon as the fish oil is withdrawn, the consumption of 2.2 lb of fish/day would have to be continued indefinitely. This does not seem feasible over a long period. One hundred grams of fish oil daily was found acceptable by patients over a period of weeks in spite of the fact that the oil was somewhat distasteful (Ahrens *et al.*, 1959). However, the consumption of such quantities of oil over a long period by the population as a whole is again unlikely. Therefore, although fish and fish oils by themselves do not appear to have much use in the dietary control of blood cholesterol levels, they may prove to be of use as part of a more general diet compiled to keep cholesterol levels low. It must be stressed vigorously, however, that before such drastic action as altering the general pattern of a nation's diet is taken, there must be conclusive evidence that such changes will reduce the incidence of atherosclerosis. At the present time, as stated earlier in this review, conclusive proof has not been obtained.

The application of vitamin A to the control of cholesterol levels has the advantage that the amount by weight of vitamin A required is small. The workers who investigated the effect of vitamin A did not report whether the depressant effect was permanent or whether the cholesterol levels rose after the treatment was withdrawn. If continual treatment at 100,000 I.U. per day is required, the toxicity, if any, of this size of dose of vitamin A over long periods would have to be studied carefully.

The sulphated alginic acid has definite possibilities as a controlling influence on cholesterol levels. It is dosed in comparatively small amounts but is currently given by intramuscular injection. It is not yet known whether the compound is effective when given orally.

It is hoped that this review has given some information of the possible application of marine products to the control of blood cholesterol concentrations. It is evident, however, that much more work will have to be done on the mechanisms involved before a clear overall picture is obtained.

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Seasonal Variation in the Collagen Content of Pacific Herring Tissues[1]

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ABSTRACT

The total amount of collagen and its relative solubility was determined in 3-year-old herring of the same population caught at two periods, June and January, representing two extremes of the sexual cycle. Sexually mature herring, caught in January, contained 40% more collagen than sexually immature fish caught in June. When fractionated into neutral salt-soluble, acid-soluble and insoluble collagen, the proportions of the three fractions remained much the same at both seasons of the year. When various tissue fractions of the fish were examined at the two seasons it was found that not only did the concentration of collagen change in the tissues with maturation but the contribution which some of the tissues made to the total body weight also changed. The skin + scales fraction contributed most to the increase in collagen in February herring. This was due partly to a higher concentration of collagen in these tissues at this season and partly to the higher proportion of skin + scales at this time of year. The significance of these findings in relation to the biochemistry of sexual maturation is considered.

INTRODUCTION

In the course of a study of differences in the physical properties of herring solubles prepared from herring caught at different seasons, it was observed that there was an increase in the gelatin content of the solubles which paralleled the development of milt and roe in the fish (McBride *et al.*, 1959a). Since herring solubles is a concentrate of water-soluble extractives obtained from whole herring, the change in its gelatin content could represent a variation with sexual maturation of either the total collagen or the solubility of the collagen present in the fish. To investigate these possibilities and to determine which tissue or tissues were giving rise to the gelatin, herring representative of two extremes of the sexual cycle were studied. Representatives of sexually immature fish (absence of visible milt or roe) caught in June were compared with fish of the same population caught in February about a month before spawning. These fish normally give rise to solubles containing respectively very nearly the lowest and highest levels of gelatin of the year (McBride *et al.*, 1959a). Analyses were made to determine the total collagen content of the whole herring and of various of the organs and tissues. In addition the total collagen as fractionated into the three forms of this protein known to exist in connective tissue: neutral salt-soluble, acid-soluble and insoluble collagen (for references see Jackson, 1957), was also determined for following how the proportions of these compared at the two seasons of the year.

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EXPERIMENTAL

The herring (*Clupea pallasi*) used in this study were representatives of a population known to frequent the area adjacent to the southeast coast of Vancouver Island (Taylor, private communication, 1960, as acknowledged). Samples of the population were obtained both in February and June at the same site of capture, Porlier Pass. The fish were frozen in dry ice immediately after capture and held at −30°C for subsequent study.

Significant changes have been reported to occur in the soluble and insoluble collagen levels during aging in albino rats (Houck and Jacob, 1958; Kao and McGavack, 1959). Age determinations were made by counting the number of annual rings on the scales according to the method of Tester (1937) and 3-year-old herring were selected for study.

For the total collagen and collagen fractionation studies, 5 males and 5 females of the February herring sample were pooled for analysis while in June, due to the absence of milt or roe in the fish, no sex differentiation was attempted and one group consisting of 10 fish was studied. Each pooled sample was first ground in a meat grinder and then homogenized in a Waring Blendor. Aliquants were removed for analysis.

For the determination of the distribution of total collagen in the herring at the two seasons, February fish were divided into 8 groups, 4 male and 4 female, each group containing 4 fish. In June, 4 groups of 4 fish of undetermined sex were investigated. Each fish in each group was partially thawed, weighed and dissected into 6 fractions. The milt or roe, when present, constituted a 7th fraction. Each of the fractions of each fish was weighed and expressed as a percentage of the whole. The corresponding fractions from each fish in each group were then pooled and homogenized. Analyses were performed in duplicate on aliquants of the homogenates.

The head was severed between the pectoral fin and the gill plate, the tail was removed by cutting at the end of the spinal cord. The skin was removed from the partially frozen flesh with the aid of a scalpel and scraped free of any adhering fat or flesh. That fraction referred to as bone consisted of the spinal cord and the rib cage. The visceral part was made up of all the internal organs in the body of the fish.

The total collagen content of the whole herring and of the dissected parts was determined by a modification of the Neuman and Logan (1950) procedure. This involves converting collagen to gelatin as well as extraction of the latter by autoclaving.

Collagen fractionations were carried out on the homogenates of whole herring using the method of Jackson (1957). In this procedure an aliquant of a herring homogenate was extracted exhaustively, first with successive portions of $0.2M$ NaCl to obtain the neutral salt-soluble collagen and then with $0.2M$ citrate buffer pH 3.5 to isolate the acid-soluble form. The extracted collagen in each fraction was converted to gelatin by autoclaving and then freed of non-gelatin extractives

using dialysis and trichloracetic acid precipitation. The insoluble collagen remaining in the homogenate after extraction of the salt- and acid-soluble fractions was converted to gelatin and then extracted by autoclaving with distilled water. Non-gelatin proteins were precipitated with trichloracetic acid.

Gelatin in all of the extracts obtained was estimated, after hydrolysis, by analyzing for hydroxyproline. Details of the procedures used have been described (McBride *et al.*, 1959a).

RESULTS

The results in Table I show that herring caught in February when very nearly mature sexually contained 40% more collagen than fish of the same age and population caught in June when no milt or roe was present in the fish. The results also indicate that there was a difference in the amount of the individual collagen fractions, particularly the salt-soluble fraction, at the two seasons of the year. However, it is apparent that the increased gelatin content of solubles prepared from February herring was due primarily to the presence of more collagen in the fish rather than to greater solubility of the collagen at this time of year.

TABLE I. Total extractable collagen and the percentage present in the neutral salt-soluble, acid-soluble and insoluble fractions in June and February herring. Each value recorded is the average and average deviation of the mean of determinations carried out in duplicate on a homogenate of 10 fish. In June, sex of the fish was not determined. In February, 5 male and 5 female fish were pooled and homogenized.

Collagen fraction	June herring		February herring	
	mg%	%	*mg%*	%
Total extractable collagen	655.3 ± 2.4	–	921.8 ± 5.3	–
Neutral salt-soluble	–	24.7 ± 0.20	–	19.7 ± 0.10
Acid-soluble	–	31.4 ± 0.63	–	34.1 ± 0.60
Insoluble	–	43.9 ± 0.50	–	46.2 ± 0.85
Percentage of total recovered in the fractions	–	95.8	–	91.4

When the fish were dissected and the various organs and tissues analyzed for their content of total collagen, the results in Table II were obtained. It is immediately evident that although herring caught in February contain more collagen, this is not present to a significant extent in either the milt or the roe of the fish, confirming a conclusion drawn previously (McBride *et al.*, 1959a). In June, the fractions containing the highest concentration of total collagen were the head, tail, skin + scales, and bone. In both male and female February fish, these same fractions, and in addition the viscera, contained the most collagen per unit weight. The greatest increases in collagen concentration in February occurred in the skin + scales and in the viscera. In the case of the viscera, however, this would appear to be due largely to the wasting away of the organs

TABLE II. A comparison of the collagen content and percentage of body weight of tissue fractions of herring caught in February and June, 1959. Results based on 4 groups in each test period totalling 16 male and 16 female fish in February and 16 fish in June. Deviations recorded are average deviations of the mean.

Tissue fraction	February female herring		February male herring		June herring	
	Collagen content	Percentage of body weight	Collagen content	Percentage of body weight	Collagen content	Percentage of body weight
	g%		g%		g%	
Head	1.61 ± 0.106	18.92 ± 1.15	1.67 ± 0.142	18.82 ± 1.05	1.39 ± 0.050	17.27 ± 0.45
Tail	2.93 ± 0.223	1.14 ± 0.05	3.49 ± 0.353	1.08 ± 0.07	2.49 ± 0.159	1.18 ± 0.06
Skin + scales	4.06 ± 0.176	8.01 ± 0.19	3.53 ± 0.217	9.52 ± 0.24	1.76 ± 0.052	6.26 ± 0.19
Bone	1.60 ± 0.172	4.51 ± 0.37	1.46 ± 0.145	4.65 ± 0.31	1.68 ± 0.124	4.15 ± 0.24
Flesh	0.31 ± 0.014	41.41 ± 1.03	0.34 ± 0.025	45.07 ± 0.94	0.22 ± 0.007	59.35 ± 0.79
Viscera	1.12 ± 0.151	2.37 ± 0.17	1.21 ± 0.100	2.83 ± 0.15	0.52 ± 0.048	11.74 ± 0.49
Milt or roe	0.033 ± 0.001	23.43 ± 1.76	0.032 ± 0.0004	17.90 ± 1.60	–	–

composing them during the maturation period, since the viscera represent a much smaller proportion of the body weight in February than in June. The skin + scales, however, not only contain a higher concentration of collagen in February but represent a larger percentage of the body weight at this time of year. It is thus evident that not only does the concentration of collagen change in the tissues with maturation, but the contribution which at least some of the tissues make to the total body weight also changes. To enable both of these variables to be taken into consideration when making comparisons of the fish at the two seasons, the data of Table II were used to calculate the contribution which each of the dissected parts would make to the total collagen content of a 100-g fish caught at each of the two periods in the sexual cycle (Table III). When the results are presented in this way it becomes evident that all of the fractions except bone and viscera contain more collagen in February than in June, with the greatest increase (approximately 200%) taking place in the skin + scales fraction.

TABLE III. Comparison of the contribution made by the various tissues to the total collagen content of a 100-g herring caught in June and in February.

Tissue	Collagen content		
	June	February	
		Male	Female
	mg	*mg*	*mg*
Head	240.65 ± 2.85	312.30 ± 10.66	301.9 ± 9.40
Tail	29.35 ± 2.49	37.70 ± 7.00	33.30 ± 2.62
Skin + scales	110.09 ± 2.84	336.10 ± 27.30	332.12 ± 7.51
Bone	69.29 ± 4.14	67.90 ± 2.39	68.90 ± 7.40
Viscera	62.88 ± 5.97	34.31 ± 3.09	26.42 ± 3.37
Flesh	130.03 ± 6.02	152.50 ± 14.37	126.05 ± 9.25
Milt	–	5.85 ± 0.52	–
Roe	–	–	7.61 ± 0.76

DISCUSSION

Proximate analyses of both Atlantic and Pacific herring have revealed marked variations in the fat and water content of various tissues depending on the time of year when the fish are caught. Milroy (1906, 1908) made the first careful study of this phenomenon in Atlantic herring and showed that the changes could be related to the feeding and spawning cycles of a given population of fish; similar relations have been found in studies of Pacific herring (Hart *et al.*, 1940; McBride *et al.*, 1956b).

The observations recorded here on the collagen content of herring at two extremes of the sexual cycle, together with the previous finding that the increase in the gelatin content of herring solubles parallels the development of milt and roe in the fish, indicates that collagen deposition in the herring is also related to the spawning cycle.

Ironside and Love (1958) have reported an increase in the insoluble protein in myotomes of cod muscle during gonad development. In the early stages at least, this increase was not accompanied by a decrease in total protein and hence appeared to represent a conversion of some soluble protein to the insoluble form. Templeman and Andrews (1956) have described a jellied condition in American plaice in which the soluble protein of the muscle was reduced. The development of this condition was ascribed to an emaciation caused by the gonads having priority in the use of protein. Although in neither investigation was the insoluble protein formed during maturation identified, it seems not unlikely that it might prove to be collagen.

The deposition of collagen during sexual maturation appears not to be uncommon among various species of fishes. One of the distinctive secondary sex characters which develop in the Pacific salmon (genus *Oncorhynchus*) during gonad development is the lengthening of the snout in the male (Hoar, 1957) apparently as the result of the deposition of cartilaginous material in the head. In one species, *O. gorbuscha*, a large hump consisting primarily of cartilage forms on the back of the male. The results reported here indicate that in herring, collagen deposition during sexual maturation takes place primarily in the skin and head portions of the body and to approximately the same extent in both males and females of the species.

The Pacific herring, like many other species of fishes, cease to feed during the terminal stages of gonad development (Wailes, 1936). It is during this period, when their body tissues are called upon to provide the substrates required for the formation of milt and roe, that much of the collagen deposition occurs. Since there is a considerable difference in the chemical composition of the tissue components and the milt and roe derived from them, one would expect the transformations involved to produce residues which, unless otherwise conserved, would be excreted. Proximate analyses of whole herring have revealed not only no loss in total nitrogen but even a slight increase during sexual maturation (McBride *et al.*, 1959b). Since nitrogen is conserved over this period it seems not unlikely

that the residues formed during gonad development are being converted to the collagen deposited.

Data obtained on the gelatin content of herring solubles (McBride *et al.*, 1959a) indicate that the collagen formed during maturation disappears within a month after the fish have spawned. The collagen deposited during maturation may thus serve as a source of energy for the herring during the recovery phase after spawning before the resumption of normal feeding. Much further work will be required to test the validity of these speculations.

ACKNOWLEDGMENT

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Comparison of Growth Rates for Native and Hatchery-stocked Populations of *Esox masquinongy* in Nogies Creek, Ontario[1]

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ABSTRACT

Recent techniques have contributed to a more accurate determination of age by the scale method and a new growth curve for the maskinonge in Nogies Creek has been constructed. Hatchery fish, planted as fingerlings, show similar growth for 4 summers after which their growth rate rapidly falls away from that for the native fish. The hatchery fish require 3 years more than the native fish to reach legal length.

A reduction in the annual growth increment for tagged fish ranges from 25% (age IV) to 80% (age VI) of that attained by untagged fish.

No significant divergence in the length–weight relationship was observed in the slower growing hatchery fish.

INTRODUCTION

Crossman (1956) reported the growth, mortality, and movement of the maskinonge, or lunge (*Esox masquinongy*), in Nogies Creek sanctuary for the years 1951 to 1953. Later studies on scale formation have led to a more accurate assessment of age resulting in a new determination of the growth curve. The present paper is concerned with two aspects of the growth of the Nogies Creek maskinonge. The growth of fish native to the sanctuary is compared to that for hatchery fish planted in the sanctuary as fingerlings and recaptured at subsequent ages. The second part deals with the effect of the preopercular disc tag on the growth increment of maskinonge.

MATERIALS AND METHODS

Each year since 1952, trap nets have been fished in Nogies Creek during May and early June, and in October. All lunge netted were tagged with a preopercular disc tag (Crossman, 1956), measured, and scale samples taken. Fish netted in the spring have been returned to the sanctuary, but those caught in the fall have been transplanted to public fishing waters. Weights were taken during several netting periods. The measurement used since 1954 has been fork length in inches, the smallest quarter inch being recorded. The mean fork lengths used in this paper are, therefore, consistently ⅛ inch less than the actual means. Crossman's measurements (standard length in cm) were converted to compare with the later data. Scale impressions were made on soft acetate slides and age determinations made with a Leitz "Trichinoskop" projector.

The recaptures to date, of 92 out of 3,192 lunge planted as fin-clipped fingerlings since 1952, has aided the interpretation of scale formation by providing

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scales from fish of known age. The use of injected lead versenate as a time mark (Fry, 1960) has met with reasonable success for the lunge and has contributed to the scale reading technique.

Consultation, in the light of this recent knowledge, has resulted in agreement between Crossman and the present writer on the criteria for age determination for the lunge. Crossman, in his original readings, disregarded what is now recognized as the first annulus. His age determinations were generally one year less than the writer's. The scales from Crossman's collection have been reread and are included in the present work.

RATE OF GROWTH

The average fork lengths for each age-group for 2,466 lunge caught during the fall nettings and 1,263 during spring nettings are shown in Table I. The designation of age-group used here is in accordance with Hile (1948). A fish in age-group II in the fall of the year has had 3 growing seasons and corresponds to an age-group III fish the following spring. By this convention, a fall fish in age-group O has completed one summer of growth. For convenience, the spring fish have been reduced one age-group, or in effect, no annulus was assumed at the outer edge of the scale.

TABLE I. Average fork lengths (inches) for maskinonge of each age-group in Nogies Creek, 1952–1959. (1 inch = 25.4 mm.)

	Age-group								
	I	II	III	IV	V	VI	VII	VIII	IX
Fall	14.0	17.7	20.2	23.3	25.7	28.5	29.6	31.8	35.9
Spring (no annulus)	15.3	17.3	20.1	22.7	25.8	27.9	30.4	32.3	...
Aggregate	14.4	17.5	20.2	23.1	25.6	28.4	29.7	32.1	35.9
Standard deviation	1.15	1.40	1.53	1.39	1.36	1.46	1.69	1.65	1.58
Number of fish	193	625	974	921	623	279	91	19	4
Hatchery recaptures	15.3	18.4	20.6	22.5	23.4	24.8	25.5		
Standard deviation	0.66	1.40	1.07	1.35	2.39	1.20	...		
Number of fish	6	21	35	12	10	7	1		

The fall and spring averages appear reasonably comparable and the data for the two periods are pooled, in the third line of Table I, to give the average length for each age-group at the end of the growing season. The fifth line shows similarly pooled data for the 92 hatchery recaptures in Nogies Creek.

Since all fish were released, differential growth for each sex was not determined. Oehmcke *et al.* (1958) reported that "five-year-old females (northern pike) will be 3 to 6 inches longer than males at that age". Clark and Steinback (1959) showed that in the first year of life male pike from East Harbour, Lake Erie, exhibit a greater growth than females, but by the end of the second year, and thereafter, females exceed the males.

Hourston (1952) demonstrated a significant sexual difference in the growth rate of maskinonge for the Eastern and Western regions of the Canadian range, females attaining a greater length at older ages than males. The lack of significant difference in the Central Region was possibly due to inadequate data for older age-groups.

The aggregate growth rate for the Nogies Creek lunge is plotted in Fig. 1 and compared with that obtained by Hourston (sexes combined) for the Central

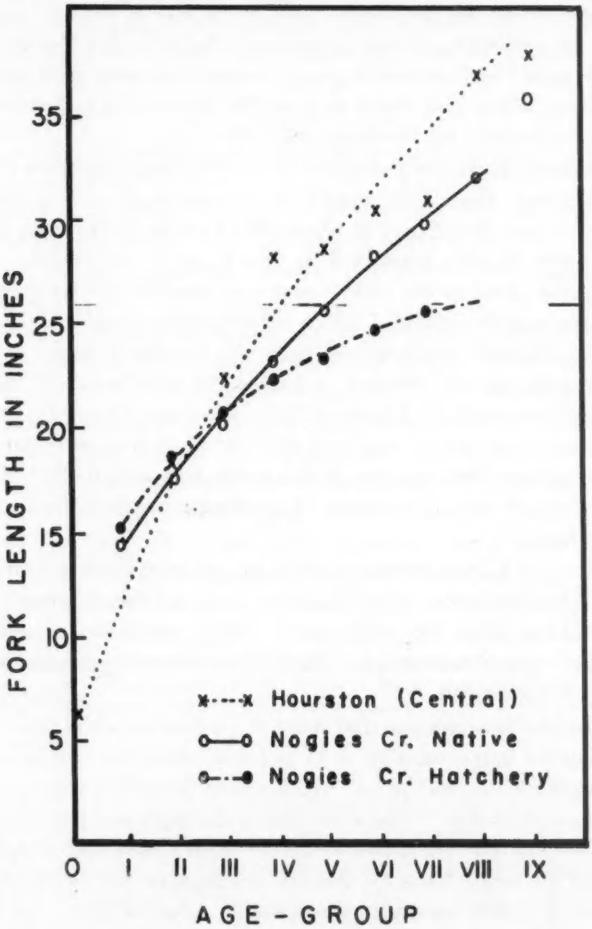

FIG. 1. Comparison of age-length relationships for maskinonge under three different conditions. Legal minimum size is 28 inches total length, equivalent to 25.75 inches fork length. Age-group corresponds to the number of completed annuli in the fall of the year (see text).

Region, which included the Nogies Creek area. The Nogies Creek lunge exhibit a greater length for the first 3 summers than lunge from the larger, nearby lakes. The two curves cross, however, at the completion of the third season (age-group II) and legal length (T.L. 28 inches) is attained 1½ years earlier in the open lakes.

The growth rate for the 92 hatchery fish recaptured in Nogies Creek is also shown in Fig. 1. These fish apparently attain a greater length than the "native" lunge in the sanctuary for the first 4 summers, after which the growth rate drops off quite rapidly and the two curves cross at the end of the 4th year (age-group III). The extrapolation of this curve indicates that the hatchery fingerlings planted in Nogies Creek require 9 growing seasons to reach legal length, whereas the native lunge attain this length early in the 7th summer and those of the open lakes (Hourston's data) by the end of the 5th.

The hatchery lunge were obtained as 4-inch fingerlings from the provincial hatchery at Deer Lake. Wild spawn is collected each year from Stoney and Buckhorn lakes, which are part of Hourston's Central Region, the major part of which is a series of lakes connected by the Trent Canal System. The Nogies Creek population, until recent years, communicated with this larger system. The three populations shown in Fig. 1 are, in all probability, genetically homogeneous.

Samples collected (by personnel from the Lindsay District of the Ontario Department of Lands and Forests), following the introduction of the species by the same hatchery stock, in Elephant Lake, Harcourt Township, indicated that the growth rate there greatly exceeded that for all three groups shown in Fig. 1. An extreme example from this lake is an average fork length of 29.75 inches for 3 lunge caught early in the 4th summer. Legal length was probably attained during the 3rd summer.

Crossman and Larkin (1959) reported that hatchery-raised yearling rainbow trout, when liberated into a wild population, attained greater length for the first 4 growing seasons than the wild trout. This observation is similar to that found for the Nogies Creek lunge. Their study, however, did not provide comparable data for older fish.

Field observations indicate that minnows and other small fish, which would serve as forage for lunge under 15 or 17 inches are extremely abundant in Nogies Creek. Larger suckers and perch, which would provide forage for older lunge are relatively quite scarce. The available food supply is a possible explanation for the observation that the native lunge in Nogies Creek attain a greater length than those in the larger lakes for the first 2 summers, but fail to maintain this status after the 3rd summer. Comparable observations, on the relative abundance of forage, are not available for the larger lakes.

By the same reasoning, the point at which the growth curve for the hatchery fish falls away from that for native fish in Nogies Creek, corresponds to the fork length at which the available forage appears to become critically reduced. It

would appear, then, that intraspecific competition in Nogies Creek could be a contributing factor to the delayed reduction in growth rate observed in hatchery fish.

The hatchery fish were recaptured from all parts of the sanctuary and no evidence could be obtained to indicate any ecological separation between the hatchery and native fish. The possibility of a missing or partially regenerated fin being responsible for the observed phenomenon seems remote since it did not interfere with growth during the earliest years. The only explanation that appears reasonable at this time is that the growth history during the hatchery phase implanted some weakness in the lunge so that they were unable to compete favourably when forage became less abundant.

EFFECT OF TAGGING ON GROWTH INCREMENT

Field observations indicated that the preopercular tag was interfering with the growth rate of the lunge. My unpublished mortality studies indicate that a greater mortality, attributable to tagging, is observed in spring-tagged lunge than in fall-tagged.

Growth during the summer of 1957 was compared for untagged lunge and for lunge tagged in the fall of 1956 and in the spring of 1957. For this purpose, no transplanting was made in the fall of 1956 but lunge caught were tagged and returned to the sanctuary. The results of this study for the year-classes 1949 to 1953 are shown in Table II. The increment for untagged fish was obtained by subtracting the average length, for each year-class, attained for fish first seen in the fall of 1956 and spring of 1957 (440 fish) from that for the fall of 1957 and spring of 1958 (409 fish). The increments shown for tagged fish are the averages of individual increments from the respective time of tagging to either the fall of 1957 or spring of 1958.

TABLE II. Average growth increments for Nogies Creek maskinonge (year-classes 1949–1953) during the summer of 1957. Standard errors are shown for the mean increments of tagged fish.

	Year-class				
	1953	1952	1951	1950	1949
Age-group in 1957	IV	V	VI	VII	VIII
Untagged fish seen before season	101	163	116	60	. . .
Untagged fish seen after season	219	125	50	15	. . .
Increment of averages	2.8	2.7	2.7	2.3	. . .
Tagged in fall 1956 and recaptured after season	18	72	60	31	15
Increment and S.E.	$2.1\pm.15$	$1.3\pm.09$	$0.9\pm.09$	$0.6\pm.09$	$0.5\pm.14$
Tagged in spring 1957 and recaptured after season	31	26	16	4	3
Increment and S.E.	$1.8\pm.18$	$1.3\pm.13$	$1.0\pm.19$	$0.6\pm.48$	$0.5\pm.15$

Figure 2 shows the plotted increments for these three groups of lunge for the summer of 1957. A reduction in the growth increment for the first season after tagging is apparent, and similar, whether the fish were tagged in the spring or in the fall. The reduction increases from 25% for age-group IV to about 80% for age-groups VI and VII. The few measurements available from recaptures after the second season indicate that normal growth was not resumed.

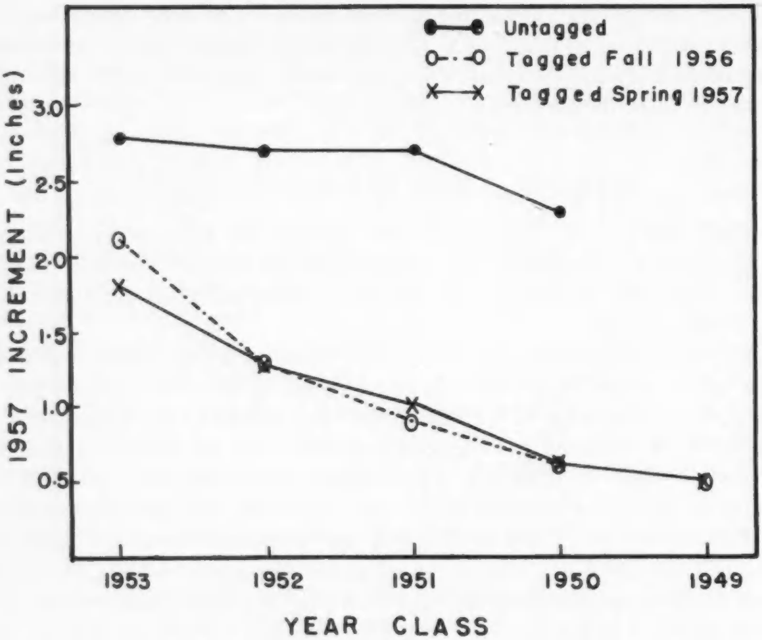

FIG. 2. Comparison of the 1957 growth increments attained in Nogies Creek for tagged and untagged maskinonge of the year classes 1949–1953.

LENGTH–WEIGHT RELATIONSHIP

The weights of the fall catch for 1956 (380 lunge) were recorded to the nearest one-tenth pound. From this catch 40 fish were selected, by tag number, using a table of random numbers (Snedecor, 1956). The formula for the length–weight regression, calculated in the manner used by Beckman (1948) was:

$$\log W = 3.285 \log L - 3.875$$

where 3.285 is the exponent "n"

and 3.875 the intercept ($\log c$).

For convenience, mean weights were calculated for 2-inch intervals and these means plotted logarithmically in Fig. 3. The line shown was drawn by inspection. Similar means for Hourston's Central Region and for the Nogies Creek hatchery fish are also shown in Fig. 3. The line drawn for the Nogies Creek native fish is common to the data for all groups.

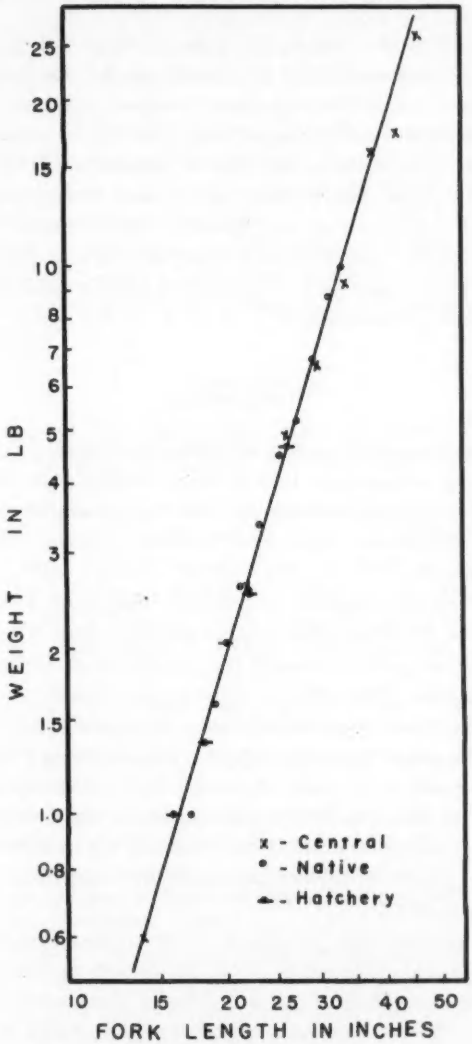

FIG. 3. Comparison of length–weight relationships for maskinonge, under three different conditions (see text) attaining different growth rates.

Equations were calculated for the means given by Hourston (Central Region only) and for the means for the Nogies Creek hatchery fish, and found to be, respectively:

$$\log W = 3.204 \log L - 3.883$$

and

$$\log W = 3.074 \log L - 3.702.$$

In consideration of the ranges of lengths involved and of the non-normality of the data, more emphasis should be placed on the line drawn by inspection through the means than on the regression constants. When a greater range of lengths is available, the data for the hatchery fish will be re-examined.

Martin (1949), in discussing the data of Karzinkin (1939), showed that the logarithmic length–weight relationship was constant for young pike reared on different diets and at different rates of growth. He indicated that several points which diverged from the line were individual cases of starvation.

No significant divergence in the length–weight relationship can be concluded for the slower-growing hatchery fish.

DISCUSSION

The results of the growth study indicate that Nogies Creek is better suited to the production of young lunge than to their maintenance after 3 or 4 growing seasons. Field observations indicate that the relative abundance of forage available for different sized lunge may be an important factor, with an overbalance in favour of smaller fish.

The reduced growth observed in hatchery fish, after 4 summers of growth at least equal to that for native fish, tends to indicate that the present techniques of hatching and rearing may preclude the possibility of favourable competition with wild populations. The reduced growth rate delays whatever value they may be to the fishery, and subjects them to an increased toll from natural mortality. Since rate of maturity generally appears to be more dependent on size than on age itself, these fish would also require a longer pre-spawning period.

Future work in this connection will include comparisons between the rate of development in the hatchery and in the field, and the factors responsible for any difference. Rapid early growth might possibly contribute to the observed unfavourable competition.

The present preopercular tagging method, although very convenient; apparently causes a considerable reduction in the growth increment and an increase in mortality. The advantage of an individually-identifiable tag for population and movement studies compensates, in part, for the undesirable effects. These effects must, however, be taken into account in the interpretation of collected data.

ACKNOWLEDGMENTS

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The collection of data was made possible only through the financial support and splendid co-operation of the Ontario Department of Lands and Forests and of the Toronto Anglers' and Hunters' Association. The interests of the latter, in the sport fisheries resources of Ontario, are responsible for the initiation and continuance of this project.

Acknowledgment is given to the invaluable direction and encouragement given by Dr F. E. J. Fry in the field work in general, and in the writing of this paper in particular. Drs L. B. Butler and W. B. Scott provided constructive criticism in the interpretation of results.

Acknowledgment is also given to the numerous undergraduate assistants and employees of the Department of Lands and Forests who have aided in the collection of data—in particular, to the endless time and patience of Mr J. C. Weir, District Biologist.

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A Population of Dwarf Coastrange Sculpins (*Cottus aleuticus*)[1]

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ABSTRACT

Cottus aleuticus in Cultus Lake, British Columbia, inhabits deep water, grows slowly to a maximum length of about 50 mm in 3 or 4 years, and spawns in the lake throughout the summer. It was taken abundantly from the stomachs of Dolly Varden char; other fish eat it only rarely. Its summer food is plankton and microbenthos.

INTRODUCTION

During 1932–1937 many examples of the coastrange sculpin, *Cottus aleuticus*, were obtained from stomachs of Dolly Varden char, *Salvelinus malma*, in Cultus Lake, British Columbia (Lat. 49° 4′ N, Long. 122° 0′ W). Specimens were determined by Dr Carl L. Hubbs and have been recorded by Dymond (1936) and others. In this lake the species is apparently confined to the deeper waters. Extensive shore seining with a long net of about ¾ inch (19 mm) stretched mesh, done in 1935 and 1936, did not yield a single specimen, though *Cottus asper* was taken regularly. Similarly the salmon fingerling traps, operated in the lake's outlet every spring at this period, took *C. asper* but no *C. aleuticus*. In examining several hundred stomachs of the other piscivorous fishes of the lake (Ricker, 1941) only a few doubtful specimens of *C. aleuticus* were found in cutthroat trout, *Salmo clarki*, and in "residual" coho salmon, *Oncorhynchus kisutch*; none were found in squawfish, *Ptychocheilus oregonense*. These species commonly forage at higher levels or closer inshore than do the char, except for the squawfish in winter. One small *C. aleuticus* was taken in a total vertical plankton haul with a No. 10 mesh Wisconsin-type net.

In deep water, however, *Cottus aleuticus* is evidently abundant. Up to an even 100 specimens have been taken from a single char, while 25 to 30 were found quite commonly in the larger individuals (300–700 mm fork length). Char were taken from the lake in every month of the year, but *C. aleuticus* were not found in them during the coldest months: March 7 to December 10 are the extreme dates of their occurrence, while they appeared regularly in the stomachs only from late March to late October.

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SIZE OF SPECIMENS

Cultus Lake *Cottus aleuticus* are considerably smaller than those of other neighbouring populations. The largest specimen examined was only 49 mm long to end of caudal fin. Dr L. P. Schultz, in a personal communication, has quoted 100 mm as the approximate maximum length of the species in Lake Washington at Seattle. McAllister (MS, 1957) examined 41 collections from British Columbia waters and found that the largest specimen was 115 mm to the end of the caudal; specimens 80 to 100 mm were quite common in these collections.

In 1934, 219 well-preserved Cultus Lake specimens were measured, taken on various dates from June 14 to September 19 (Fig. 1). The Dolly Varden, of course, eat much larger fish than *Cottus aleuticus*, including some *Cottus asper* in the 100–200 mm range. It is unlikely that they would take small *C. aleuticus* in preference to large ones, so the size of the larger fish in the *C. aleuticus* population is probably reasonably well represented by Fig. 1 (those beyond about 20–25 mm). The smallest group, represented by 2 specimens in June and about 22 in July, and with a modal length of 17.5 mm in the latter month, must be fish of the previous year's spawning (here called age I, considering January 1 as the dividing line for age designation). Age 0 fish would scarcely appear: the average diameter of a formalin-hardened ripe egg was only 0.8 mm, and spawning occurred throughout the summer.

The broken slanting lines on Fig. 1 suggest a possible *approximate* division of the 1934 material into age-groups. According to this interpretation, the char take mostly age II and age III fish; age IV, if present, is represented by only very few individuals.

It may seem remarkable that a population consisting of fish having a maximum size at about 50 mm should contain 4 or 5 different age-groups. Some might prefer to regard the "age I" fish as young of the year, to group together those now classified as "age II" and "age III" into a single category which would be age I, and to regard as age II the few fish now labelled "age IV". Against such an interpretation are the facts that (1) the size range indicated as age I in Fig. 1 increases throughout the summer and there is a deficiency of smaller sizes in August and September—which does *not* suggest continuous recruitment from the summer's spawning; (2) the present age II plus III group, if considered as a single year-class, has an unusually skewed or even bimodal distribution in the June and July samples.

SPAWNING

Information on size of mature fish was collected unsystematically. Six females carrying ripe or nearly ripe orange-coloured eggs ranged from 37 to 45 mm; 3 males with enlarged testes, from 29 to 41 mm. If the interpretation of the length groups in Fig. 1 is correct, most of the population begin to breed in their third calendar year of life.

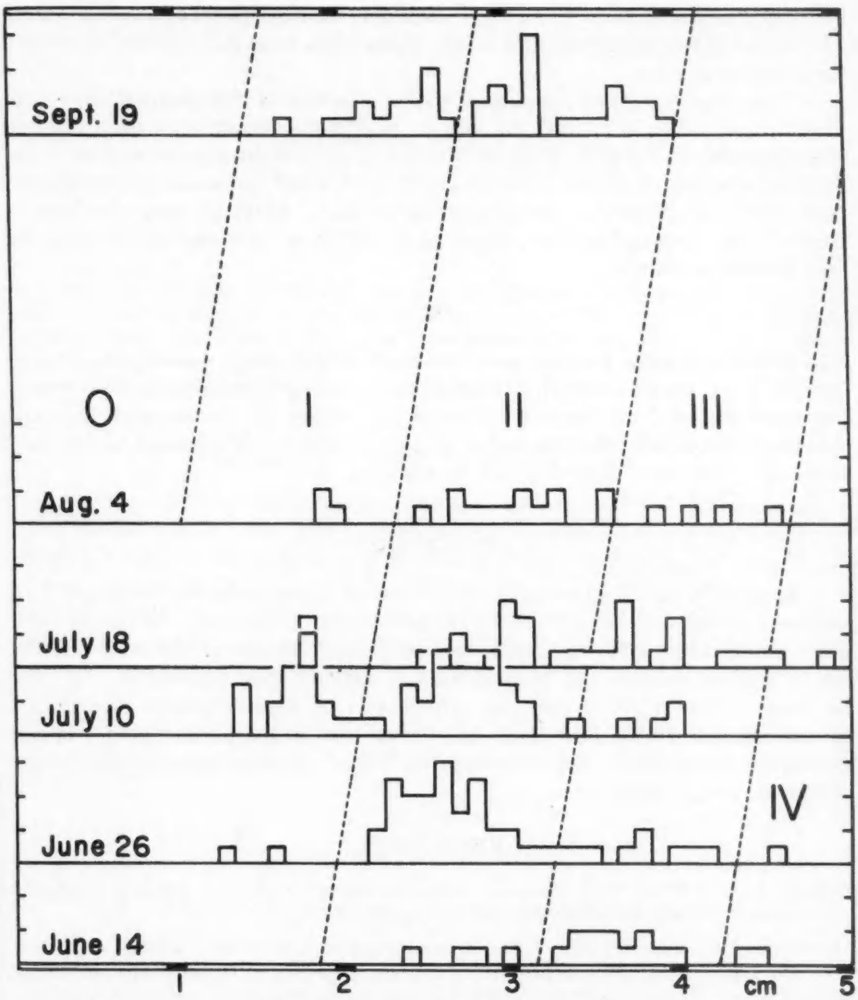

FIG. 1. Length frequency histograms for well-preserved *Cottus aleuticus* taken from char in 1934. The ordinate scale represents 2 fish and 4 days. The broken lines indicate a possible approximate separation into age-groups, as described in the text. (Lengths are to the tip of the tail fin.)

Spawning probably begins in late May or early June, although from this material it is difficult to tell exactly when eggs are first ready to be laid. By late June spawning is in full swing; it continues through July and to some extent through August. September 11 is the latest date on which a female carrying large eggs was taken.

The usual place of spawning of *Cottus aleuticus* in this geographical region is on gravel riffles of coastal streams, or in streams tributary to coastal lakes. For example, in Lake Washington the species occurs in great abundance and spawns in tributary creeks in late March or early April (personal communication from Dr L. P. Schultz). No stream-spawning *C. aleuticus* were observed at Cultus Lake, perhaps because almost all the tributary streams dry up near the lake in most summers.

FOOD

The stomachs of 16 large specimens (30–45 mm long), taken June 26 and July 10, 1934, were examined. In order of decreasing representation by volume, the food consisted of *Daphnia*, chironomine midges (17 larvae and 1 pupa), *Epischura*, Ostracoda, *Bosmina* and *Cyclops*. In addition, 1 specimen 37 mm long had eaten a smaller *Cottus aleuticus*, 14 mm long.

CONCLUSION

Apparently the Cultus Lake population of *Cottus aleuticus* is adapted to complete its whole life cycle in the deeper waters of the lake. It differs from other populations of *C. aleuticus* of the same general region in the much smaller size of the individuals, and in its prolonged summer spawning season. It may be compared with the deep-water populations of *Myoxocephalus quadricornis* (often called *Triglopsis thompsoni*) and *Cottus ricei* in the Great Lakes. It can perhaps be regarded as a population that is "relict" in an ecological sense, though not in the geographical sense.

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Further Study of Larval Herring (*Clupea harengus* L.) in the Bay of Fundy and Gulf of Maine[1,2]

By S. N. Tibbo and J. E. Henri Legaré[3]

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ABSTRACT

Plankton surveys in the Bay of Fundy and Gulf of Maine in 1958 and 1959 indicated that the largest herring spawning areas in this region are on the northern edge of Georges Bank and off the southwest coast of Nova Scotia. The drift of larvae from the spawning grounds as indicated by increasing size and by the direction of non-tidal surface currents suggest that Bay of Fundy herring stocks are supplied chiefly from the Nova Scotia spawnings.

INTRODUCTION

In continuing a program begun in 1956 (Tibbo *et al.*, 1958) plankton cruises were carried out in 1958 and 1959 to study the occurrence and distribution of herring larvae in the Gulf of Maine, Bay of Fundy and adjacent areas. This project began originally as a joint Fisheries Research Board of Canada and United States Bureau of Commercial Fisheries investigation of the "sardine" fisheries of southern New Brunswick and eastern Maine. It was later incorporated into the research program of the International Passamaquoddy Fisheries Board.

This report is concerned chiefly with the 1958 and 1959 surveys and discusses the results from the point of view of the Passamaquoddy Fisheries Investigations (Hart and McKernan, 1960).

MATERIALS AND METHODS

Table I gives details of the various cruises and larval herring collections discussed in this report.

At Prince stations (P5 and P6) both 1-m No. 0 and 12-in No. 5 plankton nets were used. Each time the stations were occupied, a vertical tow was made from bottom to surface and 15-min horizontal closing-net tows were made at 18 to 23 m and at 5 to 7 m.

The collections of the Quoddy Project (QP) and for the Bay of Fundy and Gulf of Maine series (COW-1, S-39, HS-24, HS-25, HS-27, ATC-3 and S-47)

[1]Received for publication July 22, 1960.

[2]International Passamaquoddy Fisheries Board 1956–59. Scientific Report No. 28.

[3]Present address: Instituto Oceanografico, Cumaná, Venezuela.

TABLE I. Herring larval surveys in the Bay of Fundy and Gulf of Maine during the period 1937–59.

Years	Region	Cruise or station code	Stations occupied	Frequency of collections	Net collections Tows	Net collections Larvae	Hardy recorder Distance	Hardy recorder Larvae
			no.		*no.*	*no.*	*miles*	*no.*
1937–1959	Passamaquoddy	P5	1	one per month	662	23	. . .	. . .
1937–1959	Passamaquoddy	P6	1	one per week 1937–44, one per month 1945–59	1,364	17	. . .	. . .
1957–1958	Passamaquoddy	QP	14	once per month in winter, bi-monthly rest of year except thrice-monthly Aug./57, May/58, Oct./58	602	6	. . .	. . .
1958	Bay of Fundy	COW-1	46	one cruise, Mar. 19–25	46	3	. . .	. . .
1958	Bay of Fundy (Lurcher Shoal)	L-1	1	one per week, Apr. 11–Dec. 13	47	5	. . .	. . .
1958	Bay of Fundy	S-39	11	one cruise, May 11–23	11	7	. . .	. . .
1958	Bermuda to Greenland	S-40	70	one cruise, July 21–Sept. 12	70	0	1,231	2
1958	Georges Bank (Gulf of Maine)	HS-24	4	one cruise, Oct. 7–8	4	690	. . .	. . .
1958	Bay of Fundy and Gulf of Maine	HS-25	70	one cruise, Oct. 15–30	70	285	2,796	1
1958	Passamaquoddy	EXP.	6	irregularly, Oct. 20–Nov. 21	81	9	. . .	. . .
1958	Bay of Fundy and Gulf of Maine	HS-27	67	one cruise, Nov. 10–24	67	115	755	2
1959	Bay of Fundy and Gulf of Maine	ATC-3	68	one cruise, Jan. 16–31	68	129	1,910	2
1959	St. Mary Bay	ATC-4	37	one cruise, Feb. 4–11	37	21	. . .	. . .
1959	Bay of Fundy and Gulf of Maine	S-47	40	one cruise, Nov. 5–11	40	341	386	0
Total					3,169	1,651	7,078	7

were made with 1-m No. 0 plankton nets. At each station a net was towed continuously for 5 min at each of the 20 m, 10 m and surface levels.

The Lurcher tows (L) were made by the crew of the *Lurcher Lightship No. 2* stationed off Yarmouth, N.S., at Latitude 43°48′30″N and Longitude 66°31′45″W. Two collections were made on the same day each week, one during daylight and the other at night. These were surface collections made with a 1-m No. 0 net from the anchored lightship while the tide was running strongly either at half ebb or half flood.

On the Bermuda-to-Greenland cruise (S-40) 3-level horizontal tows (20–10–0 m) and vertical tows from depths down to 200 m were made with a 1-m No. 0 net at all stations.

For the exploratory (EXP) collections both 1-m No. 0 and 12-in No. 5 nets were used. Horizontal hauls were made with closing nets at various depths from bottom to surface.

During the St. Mary Bay (ATC-4) cruise, the highspeed plankton sampler (Gulf III type) and Isaacs-Kidd trawl were used in addition to the 3-level horizontal tows with 1-m No. 0 nets.

Hardy continuous plankton recorders were towed at 10 m during some cruises (Table I).

All herring larvae collected were counted and measured. Total lengths were recorded in millimetres from the tip of the lower jaw to the end of the longer lobe of the caudal fin.

ABUNDANCE OF HERRING LARVAE

The material includes 1,658 herring larvae (Table I), 1,575 of which were taken during Bay of Fundy and Gulf of Maine cruises. The remaining 83 were taken in the Prince tows (40), Quoddy Project cruises (6), Exploratory tows (9), Lurcher tows (5), St. Mary Bay (ATC-4) cruise (21) and the Bermuda-to-Greenland cruise (2).

Although there was some bias in favour of autumn sampling in areas of known herring spawnings, Tables I and II show that there is obviously a great variation in larval abundance both seasonally and in the different areas. Nearly 90% of the larvae were taken in October and November, only 1% in May and June and none in July and August (Table II). Autumn is the principal spawning season in the Bay of Fundy and the Gulf of Maine. Six larvae, 6 to 15 mm long, were taken in June indicating that spring spawning does occur but is small by comparison with the autumn spawnings.

DISTRIBUTION OF HERRING LARVAE

Irregularities in the time of the cruises and the areas covered did not permit comparisons of numbers of larvae in the various areas by months as was done for the seasons September–February, 1956–57 and 1957–58 (Tibbo *et al.*, 1958). Several interesting points arise from the data, however, and are described here.

In the Prince tows from 1937 to 1959, 40 herring larvae were taken. Of these, 23 were taken at Prince 5, located 2–3 miles off the northern end of Campobello Island on the New Brunswick side of the Bay of Fundy, and 17 at Prince 6 located in the St. Croix River estuary. Most (29) of the 40 larvae were autumn spawned. They were caught from September to December and varied in length from 6 to 35 mm. One larva of 25 mm taken in January and 1 of 14 mm taken in March were probably the products of late autumn spawnings too. The other 9 larvae were taken in May and June. Seven of these were from 9 to 17 mm long and were undoubtedly the product of spring spawnings. The other 2 (28 and 49 mm long) may have been either fall or spring spawned.

Closing-net tows were made at Prince stations and 35 of the 40 larvae were caught at 18–23 m.

Although 9 of the 40 larvae taken at the Prince stations were recently hatched (6 to 10 mm), none of them were in the yolk sac stage and they could have drifted to the area from spawning grounds outside.

Results of QP cruises gave no evidence of Passamaquoddy spawnings either. Only 6 larvae (none newly hatched) were caught. Three larvae were taken outside Passamaquoddy Bay, 2 in the passages leading to the Bay and 1 inside the Bay. All of these larvae were autumn spawned and varied in length from 15 to 42 mm.

In March 1958 (COW-1), only 3 herring larvae were taken in 46 tows. One was taken at the entrance to St. Mary Bay, 1 south of Grand Manan and 1 at the entrance to the Bay of Fundy.

On the Lurcher shoals (L-1), south of St. Mary Bay, five larvae were taken, one (12 mm) on June 25, three (7, 8 and 9 mm) on September 3 and one (14 mm) on October 30.

A special Bay of Fundy cruise (S-39) was carried out in May 1958 to study the abundance and distribution of spring-spawned herring larvae. All of the 7 larvae taken were 39 mm or longer; 6 were taken at the entrance to the Bay of Fundy near Grand Manan and the other at the head of the Bay near the New Brunswick coast.

During the July to September 1958 cruise (S-40) from Bermuda to Greenland, the only herring larvae (2) were taken with Hardy recorders off the south coast of Newfoundland. There is no indication, therefore, that herring larvae are distributed far offshore at that season of the year.

In the October 1958 cruises (HS-24 and HS-25) in the Bay of Fundy and Gulf of Maine herring larvae were abundant (Fig. 1A). On cruise HS-24, in 4 tows made on October 7 and 8 on the northern edge of Georges Bank, 690 larvae were taken. One tow had 12, and another 678 herring larvae. All but two of these larvae were recently hatched (1 to 2% were still in the yolk sac stage) and their concentration on the northern edge of Georges Bank corresponded to the peak of hatching reported for that area in 1956 and 1957 (Tibbo *et al.*, 1958). In the second cruise (HS-25) between October 15 and 30, 285 herring larvae were found in the Bay of Fundy and the Gulf of Maine. They were most abundant on the

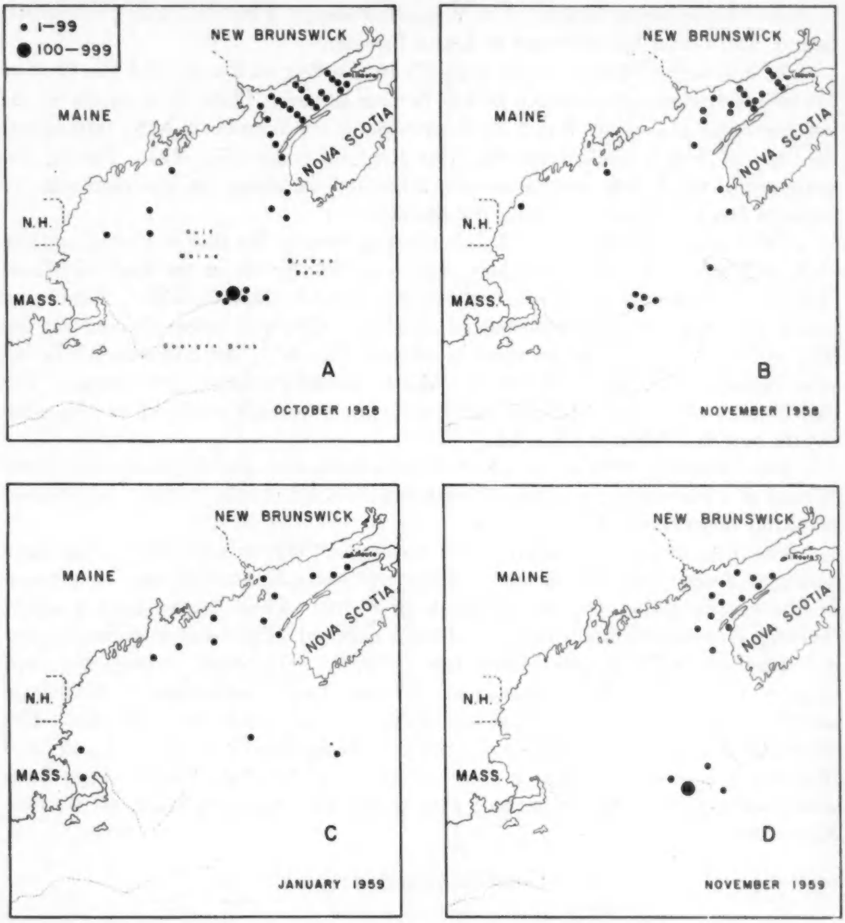

Fig. 1. Distribution of herring larvae in October 1958 (A), November 1958 (B), January 1959 (C), and November 1959 (D), in the Bay of Fundy and the Gulf of Maine.

northeast part of Georges Bank. A few larvae were taken off the tip of Nova Scotia, and along the coasts of Maine and New Hampshire. Larvae were well dispersed in the Bay of Fundy from its entrance to Isle Haute. The distribution of larvae in the Bay of Fundy was similar to that found in October 1956 and 1957 (Tibbo *et al.*, 1958).

In the 81 exploratory tows (EXP) made in the Passamaquoddy area in October and November 1958, 9 herring larvae were caught. They varied in size from 17 to 32 mm. Four larvae were taken at the entrance to Quoddy River

(north of Campobello Island), 3 in Western Passage, 1 outside near Campobello Island, and 1 near the entrance to Letite Passage.

In November 1958, a cruise (HS-27) in the Bay of Fundy and the Gulf of Maine resulted in a total catch of 115 herring larvae. These were taken on the northern edge of Georges Bank, on Browns Bank, off Yarmouth, N.S., throughout the Bay of Fundy and along the New England coast (Fig. 1B). During the same cruise the Hardy recorders took 2 larvae, one along the northern edge of Georges Bank and another along the Maine coast.

The January 1959 cruise (ATC-3) covered most of the Bay of Fundy and the Gulf of Maine. At this time there were very few larvae in the Gulf of Maine (Fig. 1C). A few were taken near Browns Bank and in Cape Cod Bay. None were found on Georges Bank. Substantial numbers (129) were taken throughout the Bay of Fundy and along the coast of Maine (Fig. 1C). An additional 2 larvae were taken in the Bay of Fundy by Hardy recorders during this cruise. The distribution of larvae in January 1959 was similar to that reported for the same month in 1958 (Tibbo *et al.*, 1958).

The February 1959 cruise (ATC-4) was limited to the St. Mary Bay area. A total of 21 larvae were taken, 17 with Isaacs-Kidd trawls, 2 with a high-speed plankton sampler and 2 in 1-m nets.

The most interesting feature of the November 1959 cruise (S-47) was the large numbers of newly-hatched larvae with the yolk sac still attached that were taken on the northern edge of Georges Bank (Fig. 1D). These larvae were 6 and 7 mm long and were probably not more than a week old. Their centre of distribution was Latitude 42°03′N, and Longitude 67°00′W. At other stations occupied near by on the same day no larvae smaller than 16 mm were taken. No larvae were taken along the Maine coast nor in other areas of the Gulf of Maine. The distribution of larvae in the Bay of Fundy in November 1958 (Fig. 1C) and 1959 (Fig. 1D) was similar to that in 1956 and 1957 (Tibbo *et al.*, 1958). They were well dispersed throughout the Bay with the largest numbers taken off western Nova Scotia.

LENGTH COMPOSITION

Length frequencies of herring larvae by 5 mm size groups are shown in Table II. About 50% of the larvae are 10 mm or less in length. More than 11% exceed 25 mm in length while less than 2% are over 40 mm. Table II shows that the numbers of larvae taken tend to decrease with increasing size. This may be due to mortality and dispersal over a wide area but there is also the possibility that the types of gear used are not very efficient for capturing the larger, more active larvae.

The mean monthly size of herring larvae increases from September to February (Table II and Fig. 2). From March to June the numbers taken are small and caution must be exercised in reaching conclusions as to when they were spawned. However, for May the size distribution would suggest a mixture of larvae from both spring and fall spawnings while in June 6 of the 7 larvae taken

TABLE II. Monthly length frequencies and monthly mean lengths (in mm) of herring larvae taken in the Bay of Fundy and Gulf of Maine.

Length	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Total[1]
mm	*no.*	*no.*	*no.*	*no.*	*no.*	*no.*	*no.*	*no.*	*no.*	*no.*	*no.*	*no.*	*no.*
6–10	...	...	...	...	...	3	...	...	8	761	47	...	819
11–15	1	...	1	...	1	3	...	...	2	32	101	1	142
16–20	1	...	...	...	1	...	...	...	...	100	180	5	287
21–25	21	1	1	...	...	...	...	...	...	67	91	4	185
26–30	28	...	1	...	...	1	...	...	...	13	22	1	66
31–35	34	10	...	...	...	...	...	...	...	1	11	...	56
36–40	33	5	...	...	3	...	...	...	...	...	1	...	42
41–45	7	3	1	1	4	...	...	...	...	...	1	...	17
46–50	5	2	...	...	1	...	...	...	...	...	...	...	8
Total	130	21	4	1	10	7	0	0	10	974	454	11	1,622
Mean lengths	32.4	36.6	26.8	43.0	36.5	13.0	–	–	9.0	10.5	17.8	20.3	

[1]Does not include 36 (7 from Hardy Recorders) damaged larvae.

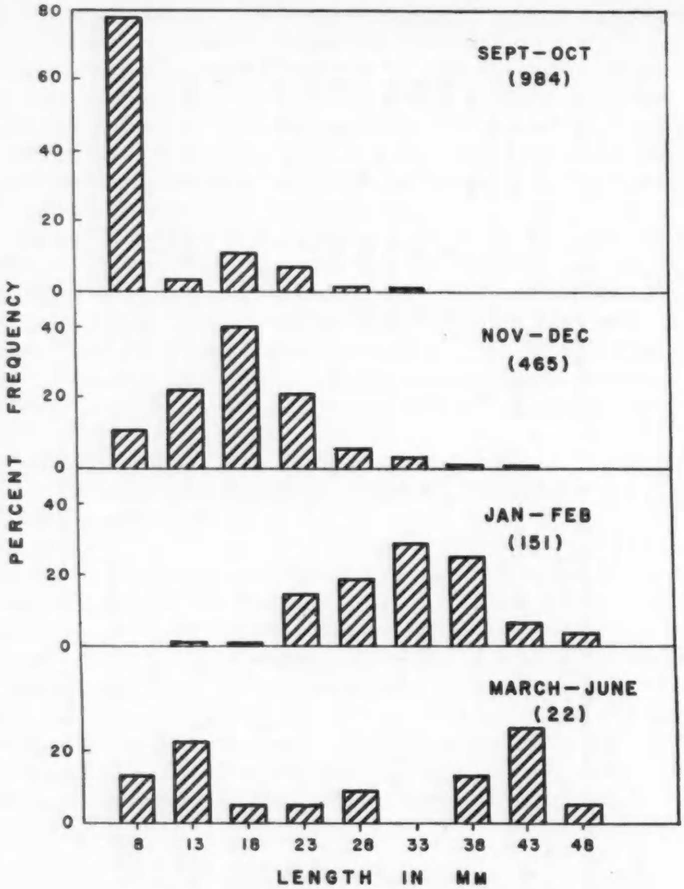

FIG. 2. Length frequency distribution of herring larvae from all cruises. Lengths are combined in 5 mm size groups.

were almost certainly spring spawned. Only at Prince 5 and 6 and the Sackville (S-40) cruise were tows taken during July and August. No larvae were caught in these months.

DAY AND NIGHT CATCHES OF HERRING LARVAE

Herring larvae were most abundant in night hauls. Their relative abundance in day and night hauls was evaluated by separating day and night tows on a 12-hr basis with the dividing points at 6 AM and 6 PM. Only those cruises which included both day and night tows were used. Table III shows the mean

catch of herring larvae for day and night hauls and the night/day ratio for each of 6 cruises. The mean catch per tow at night was greater than the mean catch during the day. The night/day ratio for all tows was 4.95. Bridger (1956) found a night/day ratio of 5.286 for North Sea herring. Because of the difference between day and night catches of herring larvae the order in which stations are occupied on successive cruises will influence the distribution pattern for larvae obtained on different cruises. Thus, caution must be used in making comparisons between cruises especially in small areas which are sampled in 12 hours or less.

TABLE III. Comparison of day and night catches of herring larvae made in the Bay of Fundy and Gulf of Maine area during 6 cruises in 1958 and 1959.

	Day			Night			
Cruise	Tows	Larvae	Larvae per tow	Tows	Larvae	Larvae per tow	Night/day ratio
	no.	*no.*	*no.*	*no.*	*no.*	*no.*	
S-39	2	0	0	9	7	.78	. . .
HS-25	38	104	2.73	32	181	5.66	2.03
EXP	57	4	.07	24	5	.21	2.97
HS-27	39	63	1.62	28	52	1.86	1.15
ATC-3	36	11	.31	32	118	3.69	12.05
S-47	21	6	.29	19	335	17.63	61.65
All tows	193	188	.98	144	698	4.85	4.95

SPAWNING SITES

Spawning sites were deduced from the location of newly-hatched (6–10 mm) herring larvae.

The collections of these newly-hatched larvae were similar to those of earlier surveys (Tibbo *et al.*, 1958) in that the products of extensive spawnings were located in the autumn on the northern edge of Georges Bank, near Lurcher shoals off Yarmouth, and along the eastern shore of the Bay of Fundy. Very few spring-spawned larvae were caught and there are not enough data available to indicate the location of the spawning areas although they are probably somewhere in the Bay of Fundy.

SUMMARY

A search for herring larvae in the Bay of Fundy and Gulf of Maine was continued in 1958 and 1959 with cruises in May, October and November 1958 and in January and November 1959. Additional data were available from the waters of southwest Nova Scotia, the Passamaquoddy area and St. Mary Bay.

Horizontal and vertical tows were made with 1-m and 12-in plankton nets. Hardy recorders, high-speed plankton samplers and Isaacs-Kidd trawls were also used.

In 3,169 tows, 1,651 herring larvae were collected. In addition, 7 larvae were taken by Hardy recorders towed over a distance of 7,078 miles.

Almost 90% of the larvae were taken in October and November. They were autumn spawned and were found chiefly on the northern edge of Georges Bank and in the Bay of Fundy.

Less than 1% of the larvae were taken in May and June. In June, 6 of the 7 larvae taken were almost certainly spring spawned.

Larvae were more abundant on the Nova Scotia side than on the New Brunswick side of the Bay of Fundy.

About 50% of the larvae collected were 6 to 10 mm in length. Less than 2% were greater than 40 mm long.

The mean length of larvae increased during the period from September to February but showed a slight decrease during the spring months with the appearance of a small number of spring-spawned larvae.

The mean catch of herring larvae per tow was greater at night than during the day. The night/day ratio was 4.95.

Spawning sites were deduced from the location of newly-hatched larvae (6–10 mm in length). Heavy autumn spawnings occurred on the northern edge of Georges Bank and on the Lurcher shoals.

ACKNOWLEDGMENTS

The authors wish to thank the masters and crews of the various research vessels for co-operating in taking collections of larvae and Mrs Delphine C. Maclellan for assistance in the examination of plankton tows and measurements of herring larvae.

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Hart, J. L., and D. L. McKernan. 1960. International Passamaquoddy Fisheries Board Fisheries Investigations 1956–59. *J. Fish. Res. Bd. Canada*, **17**(2): 127–131.

Tibbo, S. N., J. E. H. Legaré, L. W. Scattergood and R. F. Temple. 1958. On the occurrence and distribution of larval herring (*Clupea harengus* L.) in the Bay of Fundy and the Gulf of Maine. *J. Fish. Res. Bd. Canada*, **15**(6): 1451–1469.

CORRECTIONS FOR RECENT PUBLICATIONS OF THE FISHERIES RESEARCH BOARD OF CANADA

Journal of the Fisheries Research Board of Canada

VOLUME 15, No. 3—paper by Susumu Tabata: "HEAT BUDGET OF THE WATER IN THE VICINITY OF TRIPLE ISLAND, BRITISH COLUMBIA."

Page 443: The equation at the bottom of the page should read:

$$Q_\theta = \frac{\partial}{\partial t}\int_0^z \rho\, c_p\, T\, \partial z \simeq \frac{\overline{\rho c_p}\int_0^z \partial T \partial z}{\partial t}$$

VOLUME 15, No. 6—paper by S. N. Tibbo, J. E. Henri Legaré, Leslie W. Scattergood and R. F. Temple: "ON THE OCCURRENCE AND DISTRIBUTION OF LARVAL HERRING (*Clupea harengus* L.) IN THE BAY OF FUNDY AND THE GULF OF MAINE."

Page 1455: Table I, line 1, instead of 1942–1957, read 1942–1958. Line 2, instead of 1946–1957, read 1946–1958.

VOLUME 16, No. 6—paper by J. G. Hunter: "SURVIVAL AND PRODUCTION OF PINK AND CHUM SALMON IN A COASTAL STREAM."

Pages 878 and 879: The captions of Fig. 10 and 11 should be interchanged.

VOLUME 16, No. 6—paper by M. W. Smith: "PHOSPHORUS ENRICHMENT OF DRAINAGE WATERS FROM FARM LANDS."

Page 893: Last paragraph, the sentence beginning in line 6 should read "Young *et al.* (1959) give a summer value for phosphate phosphorus in the surface water immediately outside Malpeque Bay, to which . . . ."

VOLUME 17, No. 1—paper by D. R. Idler and I. Bitners: "BIOCHEMICAL STUDIES ON SOCKEYE SALMON DURING SPAWNING MIGRATION. IX. FAT, PROTEIN AND WATER IN THE MAJOR INTERNAL ORGANS AND CHOLESTEROL IN THE LIVER AND GONADS OF THE STANDARD FISH."

Page 113: Abstract, line 6, instead of "0.5" read "1.4"; line 7, instead of "8" read "15".

Table II: Instead of "Protein, grams" read "Protein N, grams". This error makes several corrections necessary in Table III and the discussion of Table III.

Page 118, para. 6, line 1, "protein" should read "protein nitrogen".

Page 119, para. 6, line 1, instead of "11" read "34.4"; line 3, instead of "0.47" read "1.44"; line 4, instead of "1.39" read "8.63".

Page 119, para. 7, line 1, instead of "229" read "425"; line 2, instead of "8.1" read "15.1".

Table III, under heading "Protein" read "–2.50" for "–0.4"; "–1.88" for "–0.3"; "–40.0" for "–6.4"; "–38.8" for "–6.2"; "–0.24" for "–0.04"; "–3.13" for "–0.5"; "+27.5" for "+4.4"; "+234" for "+37.4"; "trimmings" to read "trimmings*".

Page 120, para. 2, line 2, "2.7" to read "4.3"; line 4, "2.0" to read "13.4"; line 5, "1.7" to read "3.0"; "1.0" to read "9.0".

Page 120, para. 3, line 2, "88.2" to read "88.8"; line 3, "99" to read "93.6"; line 4, "90.6" to read "89.7"; "91.0" to read "90.8"; "88.6" to read "88.5".

Page 120, para. 4, line 6, "3.4" to read "5.5"; line 7, "2.1" to read "12.9"; line 8, "2.3" to read "3.9"; "1.9" to read "12.0".

Summary: Para. 3, "15" to read "11"; para. 5, "8" to read "15"; "0.5" to read "1.4".

VOLUME 17, NO. 1—Note by Gordon C. Pike: "PACIFIC STRIPED DOLPHIN, *Lagenorhynchus obliquidens*, OFF THE COAST OF BRITISH COLUMBIA."

Page 124: The sentence beginning in line 3 should read "In March, 1958, off the coast of California, two fur seals were seen with Risso's dolphins, striped dolphins and right whale dolphins from the M.V. *Trinity*, by scientists of the United States Fish and Wildlife Service who were engaged in fur seal research."

VOLUME 17, NO. 2—paper by R. A. McKenzie and S. N. Tibbo: "HERRING FISHERY IN SOUTHERN NEW BRUNSWICK."

Page 143: Table IV, the column heading "Grand Manan" should read "Saint John County", and vice versa.

Progress Reports of the Atlantic Coast Stations of the Fisheries Research Board of Canada

ISSUE NO. 72—Article by Neil J. Campbell: "AN INTERNATIONAL GEOPHYSICAL YEAR PROJECT."

Page 33: Fourth line under the heading SALINITY, for "(1150 fathoms)" read "(1640 fathoms)".

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